Vadim Sidorovich and Irina Rotenko

Reproduction biology in grey wolves *Canis lupus* in Belarus: Common beliefs versus reality

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This scientific monograph gives a detailed information about reproduction biology in the grey wolf *Canis lupus* in Belarus. This topic includes the wolf breeding (mating and denning) behavior, fertility of the species and mortality of its pups. The initial material was not collected occasionally from wolf hunters and wolf pup searchers, but mainly gained by authors first-hand according to a well-set research design and long-term. By analyzing the gathered data, we became convinced that in the wolf reproduction biology there are more exceptions than rules. Therefore, the standard patterns of reproduction biology in wolves that are wide-spread in the published literature about the species we call as common beliefs that are given versus the wolf reality that we have found in Belarus. Concerning the non-standard features in the wolf reproduction biology, we revealed that multiple breeding in wolf pack is a common phenomenon, breeding of yearling females and wolf-dog hybridization were found to be irrespective the food base and strongly depending on the *species population density* i.e. they are reproduction regulations. Wolf pup mortality was investigated and the crucial role of deliberate predation by lynxes and trampling by wild ungulates on wolf pups survivalship was revealed. Behavioral adaptations of wolf breeders against the reproduction failure were found out.

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Preface

Wolves are not an easy research subject. Elusive, often nocturnal, moving fast across huge areas and often difficult terrain, wolves have challenged researchers, hunters, nature lovers who have been trying to observe them in the wild. The difficulty to track them is part of the fascination that has attracted humans to this species throughout human history. In the early 70s, the irruption of radiotelemetry among the suite of technicalities used by wildlife biologists dramatically increased the wealth of data and insights collected on many aspects of the biology of wolves as well as other predators. Several thousands of wolves have been radio-collared in many parts of their large range across the northern hemisphere and all aspects of their biology have been investigated. One would easily conclude that there is very little left to be studied and learned on wolves but this would be a great error, as clearly shown by this book by Sidorovich and Rotenko. There are at least two main reasons making this book exceptionally interesting to wolf scientists.

Luigi Boitani, professor, doctor of biology, Sapienza University of Rome, Italy, 2015.

The first reason is that this book reveals previously unknown aspects of wolf reproduction, such as the high frequency of yearling reproducing females and of multiple litters in the same pack. It is true that wolves are extremely adaptable to a variety of habitat types, prey base, human pressures to the point that every new study in a new geographic area is likely to yield new results. However, none really knows the limit of this ecological and behavioural flexibility and this book reports on wolf biology in a very unusual setting: for example, wolves in Belarus are heavily hunted

and have to face the fierce competition of lynxes preying on their litters.

The second reason is that this book is the result of the incredibly intensive field work done by Vadim Sidorovich and Irina Rotenko for many years and in two study areas. The number of litters found, of kilometres of snow and mud-tracking, of hours of observation, the numbers of wolves followed throughout their lives and, in general, the quantity of data gathered during so many years has little or no comparison among wolf research projects. The authors reveal an unusual capacity for the field work and a natural sense for the real life of wild wolves. Their exceptional dedication to gathering first hand data in the field has produced excellent sample sizes for many of their analyses even where qualitative statements are privileged over data munching and modelling. The result is a book to be read as a combination of a scientific report and a personal account of living in the forest in close companion of wolves. Among hundreds of anecdotes, a consistent and forceful story of the life of wolves in the forests of Belarus emerges to be compared with the well-established scientific information available for wolves of North America and western Europe. Scientists will have some difficulties in using this book, because data are often offered in unconventional formats. However, the quantity of data and the obvious great knowledge and practice of the authors on their subject provide strong support to their conclusions.

Luigi Boitani

Chapter 1. Introduction

The introduction of this book about the grey wolf *Canis lupus* reproduction biology was mostly written by one of the authors, Vadim Sidorovich, who initiated, designed and carried out the main part of the below-given studies on wolves in Belarus. Irina Rotenko, who is the second author, helped me with wolves really a lot. From 2005 until 2010 all work was done together with her. From 2011 until 2017 she still assisted me with the studies on wolves despite the fact she was busy with other matters. Many other persons, who assisted somehow in the wolf studies are mentioned in the acknowledgements.

This introduction consists of three parts. The first part is about our aims and motivations to write this book. The second part highlights the new knowledge and skills that were represented in the book. Finally, I would like to thank and mention all the persons, who really helped me in this not easy study, *i.e* the third part is acknowledgements.

Thinking about the aims and motivations, as well as about the originality in the book messages, I would like to say the following in several theses.

(1) *Vadim Sidorovich, predator researcher of the Naust ecostation, doctor of biology since 1989, professor since 2008. Naliboki Forest, 2017.*

Being an amateur of wildlife and a professional zoologist, I was caught by passion of learning reproduction in wolves, first of all, the species denning and family life. Over two decades we quite successfully searched for the wolf dens in Belarus (mainly in Paazierre Forest and Naliboki Forest) and marked many of the found wolf pups by finger clipping, then we traced the marked wolves for as long as possible. Also, in Naliboki Forest we traced the reproduction in wolves against the background of the recolonisation of the forested terrain by lynx-

es up to the stage of outstandingly dense lynx population. It appeared that lynxes impacted the reproduction in wolves dramatically, and this study on the lynx-wolf interactions brought very interesting new results, too. All these allowed us to collect a quite unique data set in relation to reproduction in wolves. So, the first and main idea for the book was just to share the gained knowledge and skills with wolf colleagues and amateurs.

In accordance with the main idea for the book, I have no ambitions to analyze and synthesize on the topic for the whole (large and ecologically various) distribution range of the species. Therefore, in this book you will not find a comprehensive review of the literature in relation to the wolf reproduction and social behavior, which combine our own data with data and knowledge gathered worldwide. Although I could do this, I prefer to study the species in the

(2) *Irina Rotenko, predator researcher of the Naust ecostation, Naliboki Forest, 2017.*

wild, getting answers on small questions about behavioral and ecological details. An analysis of all the published results on the topic simply demands too much time at a computer screen, which is not how I wish to study wolves as well as is not my life choice generally.

As to the absence of such a review, I also did not that because of my evident problem with English. I hope the readers of this book will take into account I am not a native English speaker and have never visited any English courses even for a day. I simply had other priorities, and one of them brought this book. Moreover nowadays, when there are so much information published on most of questions, a review of results up-to-date is getting more and more as a separate job in relation to a reporting of a study results.

One may ask why we have written this book, without publishing a series of articles for zoological journals. There are several reasons for that, and I would like to tell about them. Nowadays, articles in such journals are under such heavy reviewing, and, in turn, they demand too much time, leaving not enough time for the study itself. It appears a temptation to economize life time and neglect such journal system. Therefore, in order to advance in my research and life objectives I chose an alternative way. To share research results with colleagues, we chose to create books and make them available for everyone, free on the Web. It seems to be a good alternative way and web stats support this choice.

Moreover, some other peculiarities of our approach do not facilitate publishing in zoological journals. We avoid excessive use of statistics, mathematical simulation *etc*. Instead we try to provide enough proof not with abundance of figures and complicated statistics, but by using many suitable documented examples. We limit the use of estimates and statistics to a minimum, but attach great importance to detailed and high quality basic data. This is how we believe zoology should be. We have no affinity with zoologists, who hide their lack of knowledge behind too many estimates, statistics and mathematical modeling. To our regret, such zoologists are getting more and more common in the modern city-biased world.

Also, we avoid ambiguous and too sophisticated terms for a still unclear phenomenon. Therefore, for instance, in this book about the wolf reproduction we did not use the terms 'rendezvous site' or 'adoptee'.

On the other hand, by comparing the creation of a book and the writing of a scien-

tific article, we immediately realize the main advantage of books. In a book one can describe or illustrate something thoroughly and without limitations, and give the reader access to all results in one.

There was another aim and motivation to do this book. By investigating the publications in relation to the grey wolf, we noticed that our results may bring quite a lot of new knowledge on the species reproduction biology in the region of the European forest zone, and this encouraged us to publish the results.

There is a lot of knowledge about the wolf breeding behavior and denning in North America, but the behavioral patterns differ a lot from those in Europe (Mech & Boitani, 2003 and references therein; Sidorovich *et al.*, 2017). Reading the literature about grey wolves and talking with colleagues about the species in North America, comparing that with my experience and knowledge gained in Belarus, I became convinced that wolves in North America and Europe are very distinctive in their behavior, almost as if they are two different species.

We may mention two simple examples.

As to the wolf breeding behavior, in North America breeding wolves permit humans to observe them at the den by keeping a security distance (*e.g.* Mech, 1988; Mech & Boitani, 2003). Quite opposite, in Belarus breeding wolves often immediately escape with their pups from the denning area, if people enter from a road into their denning habitats. Even, if people pass still quite far (300-700 meters) from the wolf den, they move their pups to another denning area, at least, several kilometers away. In Belarus, breeding wolves never use one den for a long time like in North America. Quite opposite, during the first 30-50 days of pup raising, parent wolves keep pups in several denning sites with many used dens in each denning site (up to 79, usually 15 to 30) by replacing pups frequently (Sidorovich *et al.*, 2017).

Concerning the intraspecific aggression, in North America wolves are often aggressive towards each other and it's not rare if a wolf gets killed by another wolf (Mech & Boitani, 2003). In Belarus and seemingly in the whole of Eurasia such strong aggressive encounters are rare. After almost four thousand kilometers of snowtracking of wolves in Belarus we never faced with this. Moreover, among almost seven hundred carcasses of wolves inspected, we found very few wolves with traces of fights with other wolves. However, once in winter (late

January) at a forest road, we discovered a relatively small male wolf with an injured hind paw, which was killed by another wolf.

We will briefly discuss the possible causes for such differences in the wolf traits in Eurasia and North America. Wolves in North America and in Europe or wider in Eurasia were isolated for an evolutionary long enough time to be distinctive; the species lived and evolved in different habitats with different prey stock. Moreover, wolves were extirpated over most of their North-American range, later followed by reintroduction and spontaneous recolonization of large areas (*e.g.* Paquet & Carbyn, 2003). During wolf expansion in North America hybridization of wolf with stray dogs and coyotes could frequently happen. Another great difference is that the indigenous people, *i.e.* native North Americans have never persecuted wolves, and only the European invaders and then the new Americans began extirpating wolves in North America about two centuries ago.

Conversely in Belarus, Eastern Europe and further eastwards wolves were strongly persecuted for a considerably longer time: at least since the 16th century. At the same time, despite of the longer and heavy wolf persecution by humans, wolves in Eurasia have never been extirpated on such a large spatial scale as in North America. Another example is hybridization of wolves with stray dogs. Again conversely to North America, hybridization was a rare phenomenon in Belarus, at least, until the early 2000's. European study on wolf genetics revealed that at that time the wolf population in Belarus displayed very little genetical contamination by hybridization with stray dogs; none of the genetically investigated wolves from Belarus showed dog ancestry (Stronen *et al.,* 2013). Various other differences between North American and European wolves were already discussed in earlier literature (Jędrzejewski *et al.,* 2010).

Published studies on wolves in other regions of Europe such as Eastern Poland, Russia, Fennoscandia, Italy (*e.g.* Bibikov, 1985 and references therein; Jędrzejewska *et al.*, 1996; Jędrzejewska & Jędrzejewski, 1998; Jędrzejewski *et al.*, 2000, 2001, 2002, 2007; Mech & Boitani, 2003 and references therein for Italy and Fennoscandia) are basically characterized by detailed results on foraging and diets, impact on the prey populations, home range and territoriality, movement and population dynamics.

Concerning studies on the wolf breeding in Europe, there are several publications on the topic (Bibikov, 1985; Theuerkauf *et al.,* 2003; Schmidt *et al.,* 2008). Wolf denning behaviour in the European forest zone was described in two articles for the area of Bielaviezha (Białowieża in Polish) Forest, the Polish part (Theuerkauf *et al.,* 2003; Schmidt *et al.*, 2008). However, the articles were based on telemetry study with few breeding females (n=6) and a rather small number of investigated dens (n=8 and 16). Therefore, in our point of view, the mentioned results might bring a simplified and biased knowledge on the topic (see Chapter 4 for details).

A lot of information on the wolf breeding in Russia has been published (*e.g.* Bibikov, 1985; items and references therein, first of all, Danilov *et al.*, 1985), but those studies were mainly based on data that was gained from hunters and wolf pup searchers. For our part, there is no doubt that data collected by hunters are not sufficient and may be greatly biased. Having both our own data and data from hunters in Paazierre Forest, we became convinced of this. For instance, if a hunter reports a discovered wolf litter, it's hard to be sure, if the possibility of multiple breeding in the wolf pack was sufficiently checked.

The results on wolf denning behavior in the European part of Russia (Danilov *et al.*, 1985) are of short descriptive nature. Actually, the authors (Danilov *et al.*, 1985) did not consider denning behavior as the main aim of their study on wolf reproduction. Their research was targeted on the effect of the wolf breeding on their demography as well as on fertility in wolves. On these questions the results gained by the Russian authors were a great advance in the study on the wolf reproduction.

Anyway, taking everything into account, we can conclude that before the given study in Europe and even in Eurasia nobody from zoologists investigated the grey wolf breeding and overall reproduction systematically on a large set of own-gained data that were gathered through a scientifically sound approach. Therefore, despite of the presence of the above-mentioned publications we state that actually there is not much correct knowledge about denning in wolves in the European forest zone.

Our data on the wolf breeding in Belarus was collected from two local populations of wolves (in Paazierre Forest and Naliboki Forest), on a regular basis during a long period. In effect, a very extensive set of data on wolf reproduction, in particular on

aspects such as fertility, denning behavior, reproductive regulations, diet of pups, survival and mortality of pups were collected. Quite a lot of interesting information was gained by pup finger clipping and subsequent tracing of such marked wolves with their specific footprints. In addition, smart use of many camera traps (up to 70) during just five years brought some exciting results.

One of the motivations to prepare this book about the wolf breeding was that in Europe and wider in Eurasia there is a widely spread belief that the species is strictly monogamous with a certain way of breeding and pack formation in family pattern (*e.g.* Bibikov D.I., 1985 and references therein; Jędrzejewska & Jędrzejewski, 1998).

Actually, in our study in Belarus since the late 1990s we have found so many abnormalities, that we start thinking about what actually prevails in the wolf reproduction: the "rules" or "exceptions". Such "abnormalities" occurring often is a very interesting phenomenon. To describe and analyze these was another important goal of the book.

There are several commonly accepted and seemingly 'normal' features of the wolf reproduction biology and the species pack forming in the Eurasian forest zone (Bibikov, 1985; Mech & Boitani, 2003 and references therein). Below a list of these "rules", or should we say "common beliefs"?

(1) The first breeding of female wolves happens, when they are about two years old or older.

(2) During breeding season, a wolf pack has merely one litter or there are no pups.

(3) Usually a wolf pack consists of parent wolves and their pups of the current and previous biological years as a normal maximum; additionally, such a pack may subordinate some non-relative wolves.

(4) Usually offspring disperse from their maternal pack around mating season, in the second year of their life, when they are 20-22 months old.

(5) When wolves are more or less common, they usually kill and even consume stray dogs, but do not incorporate them into a pack and do not interbreed with them. Pairing with stray dog happens in a rarefied wolf population; and both sexes of stray dog may be paired with both sexes of wolves, respectively.

(6) There is nearly nothing mentioned about a great negative role of the Eurasian lynx *Lynx lynx* and wild ungulates (mostly elk *Alces alces*, red deer *Cervus elaphus* and bison *Bison bonasus*) on the survival of wolf pups. There is a common belief that these animals do not markedly impact wolf reproduction.

In our study we found that (2), (3) and (4) are only partially correct, there are exceptions of (1) and (5), while (6) is entirely the opposite.

The following 'abnormalities' were found in Belarus:

(1) Pack multiple breeding appeared to be a common phenomenon in Belarus. Indeed, during 20 years of investigating wolf breeding in Naliboki Forest and Paazierre Forest we found 74 dens with pups ourselves. Searching for wolf dens and while investigating denning of wolves with camera-traps as well as by means of registration of pup presence by their tracks, a total we learnt more or less sufficiently about denning in 59 wolf breeding groups. During this study we revealed 17 cases of double breeding and 2 cases of triple breeding in a wolf pack (actually in a wolf breeding group *i.e.* a couple or larger breeding group up to five adult wolves). So, at least, in 32% of the investigated denning cases there was registered a multiple breeding phenomenon in wolf packs. The main reason for multiple breeding was mating of the dominant (founding) male not only with the founding female (mother), but with daughters or other subdominant females. Taking into account that not in all cases the possibility of multiple breeding was checked sufficiently detailed, *i.e.* when other possible litters could be not discovered, we assume that actually multiple breeding in wolf packs occurs even more often than can be derived from our data.

(2) Pup survival may be extremely low, and quite often whole litters die.

(3) Out of 74 wolf dens with pups, breeding of yearling females was revealed for two times (3%). Considering the ratio between yearling and other females in the wolf population, the data suggests that approximately 5-8% of yearling females already breed.

(4) Timing of parturition in the wolf population seems to be getting prolonged or there are just many exceptions. In the 2000's among 63 well-documented parturitions, we registered one parturition in mid-January, 4 parturitions in late March-early April and 4 parturitions in the last ten days

of May. The majority of the registered parturitions in wolves were dated within a normal seasonal period, *i.e.* the last ten days of April till mid-May.

(5) Also, we gained enough proofs that lynxes suppress the wolf reproduction a lot by deliberately hunting on vulnerable individuals such as pups of the year, yearling females and heavily pregnant females. Wild ungulates kill many wolf pups, as well.

(6) We frequently found peculiarities of pack formation. One of them is offspring that stayed with their parents for 3 to 5 years without breeding. The opposite trend is pack formation by mostly unrelated wolves (without direct family ties). This is connected with pack deterioration through wolf persecution by humans or/and because of extremely low survival of pups. Both situations lead to pack formation with non-relatives, sometime during autumn, when strong wolves gradually subordinate other non-relative wolves that are ranging around. In such situations the majority of wolf packs in winter mostly consisted of non-relative individuals without pups of the year.

(7) Among seven well-documented cases of hybridization between wolf and stray dog (all recent cases), three cases were registered in Naliboki Forest, when the wolf population was quite dense. In all seven cases it was a naturalized female stray dog and a male wolf that created the hybrid family.

The book structure is as follows. Chapter 2 describes study areas, which we use to investigate reproduction in wolves in Belarus. Chapter 3 gives the methods, which were applied to study on wolves in Belarus: method of wolf census and approach to estimate the species population density; snowtracking of wolves and identification of wolf tracks; collecting information from the individual wolves that were marked with a clipped finger; wolf pup searching and study on wolf denning behavior; estimation of wolf fertility parameters; investigation of wolf pack composition; study on the interference between wolves and lynxes; gathering of scats of wolf pups and their parents, analysis of the scats in order to estimate the pup and parent diets; determination of wolf age; estimation of the population density of the main prey species; statistical methods. In chapter 4 we analyze breeding behavior in wolves: mating in wolves; wolf denning and tending of early days pups; raising of pups after weaning; and some

behavioral traits of wolf-stray dog pairs at denning and raising pups. Fertility and reproduction regulations in wolves are given in chapter 5. In this chapter we address to the frequency of breeding in female wolves and its density-dependent variation; fecundity and its density-dependent variation; pack multi-breeding as a density-dependent reproduction regulation in wolves; and hybridization with stay dogs as an overexploited population response to compensate the loss. Chapter 6 investigates the mortality in wolf pups with implication for the species population structure: mortality causes and estimates of mortality rate in wolf pups as well as the decline in the wolf reproduction with implication for wolf pack composition. Chapter 7 suggests on the trends in the denning behaviour of the wolf in connection with the changes in the vertebrate community in Naliboki Forest, or by other words how wolf breeders try to adapt to the new unfavorable situation with denning *i.e.* too many lynxes, bison, red deer and other wild ungulates. At the end we give the basic results and list of references.

In the chapter about the methods, which we applied to study wolves in Belarus, we describe how we search for wolf dens. This method is one of the results of our work and experience with wolves as well. Of course, there is no doubt more people have been searching for wolf dens in Belarus. Some of them were quite successful wolf pup searchers, and I learnt skills from two of them. Gradually I got convinced that the way they searched for wolf dens was not substantiated enough, and the method could still be developed considerably. I have worked on the refinement of the method for longer than ten years and finally those efforts resulted in the substantiated procedure of searching for wolf dens which is described in the methodology chapter. In connection with this, I am very grateful to the wolf pup searchers Viktar Staliarow and Aliaksandr Huryn, from whom I really learnt a lot. Of course, not all the small details (*e.g.* intuition) that I used for wolf pups searching it is possible to describe.

An essential part of the given results have been gained thanks to the financial support that was provided by the Institute of Zoology, the National Academy of Sciences of Belarus in 1984-2008 and in 2009-2017 by the Scientific-Practical Centre for Biological Resources, the National Academy of Sciences of Belarus. The study on wolf reproduction biology advanced a lot, when we worked

(3) *Aliaksandr Hurin, professional hunting warden and wolf pup searcher. The Kalienkavichy district, Homiel' region, 2006.*

for the three year (2006-2008) state project to elaborate the management plan of the wolf population in Belarus. This was a special project within the state Program to develop the game economy in Belarus. Afterwards, the next significant steps on the way to investigate reproduction in wolves in Belarus were two recent (since 2014) projects of the Centre for Biological Resources: one on the wolf reproduction and another on hybridization of wolves with stray dogs in Belarus. We are very grateful for all these financial supports that provided important advance in the given studies.

At the same time, during a quite long period (1985-2005), before our first project on wolves in 2006-2008 in the Centre for Biological Resources, the National Academy of Sciences of Belarus as well as in 2018 and 2019 I (we) gradually pushed the study on wolves in Belarus forwards by

investing my (our) own efforts and private money and time as much as I (we) could. A similar situation was in the period from 2009 till 2014, when in some years (particularly 2011-2013) we had almost no possibility to study on wolves in the Centre for Biological Resources. Nevertheless, even in this period between the mentioned larger state projects on wolves we had several smaller wolf-related projects such as one from Epo-film, Wien, Austria in 2010 and from Andreas and Eva-Mayr STIHL Foundation in 2008-2010. We are very grateful for these financial supports that provided a lot of advance in the studies on wolves in Belarus as well.

Julia Holikova helped with analysis of pup diet and census of pups in early autumn. John Griffiths, Maximilian Hetzer, Jan Gouwy, Annick Schnitzler and Sanne Ruyts assisted with searching for wolf dens in some years. The team from Wild Naliboki (naliboki.org), personally Jan Gouwy, Sanne Van Den Berge and Sanne Ruyts assisted with camera-trapping. Also, Maximilian Hetzer helped with camera-trapping. Sanne Van Den Berge, Annick Schnitzler and Jan Gouwy helped with proof reading.

Also, in this acknowledgment part we would like to thank a number of hunters

(4) *Victar Staliarow, professional hunting warden and wolf pup searcher. The Shumilina district, Vitebsk region, 1997.*

and hunter wardens, who helped a lot with providing possibilities to investigate wolf carcasses, first of all, Viachaslaw Kazenka, Lienard Jurevich, Baliaslaw Sadowski, Viachaslaw Budny, Victar Staliarow, Uladzimir Lukshyts, Jahor Makieienak, Ihar Lutkowski, Uladzimir Litsvinaw, Alieh Sidarenka, Uladzimir Ivanowski, Raman Pasrednikaw and Aliaksiej Blinaw.

Chapter 2. Study areas

Mainly, two wide-ranging forests were used for the study (Map 2.1). The first one, called Paazierre Forest, is situated in the northern part of Belarus in the Vierkhniadzvinsk, Rasony, Polatsk, Shumilina, Haradok and Vitebsk districts of the Vitebsk region *e.g.* 55º58'N, 28º22'E.

The second one, the Naliboki Forest, is situated in the central-western part of Belarus, in the districts of Valozhyn, Iwie, Navahradak and Stawptsy of the Miensk or Harodnja regions, *e.g.* 53º55'N, 26º20'E.

2.1 Paazierre Forest

Paazierre Forest is a part of the extended region within the European forest zone, which is characterized by a transitional structure of forests and located between more southern deciduous (mostly broad-leaved) forests and boreal coniferous forests. The spruce *Picea abies* and pine *Pinus sylvestris* are the dominant coniferous trees. The black alder *Alnus glutinosa* and grey alder *Alnus incana*, birches *Betula pendula, Betula pubescens* and aspen *Populus tremula* are the most common deciduous trees there.

The climate in Paazierre Forest is humid continental. Winters are characterized by snow cover, with average air temperature below 0ºC. The snow cover usually persists for at least 1.5-2 months, with a maximum depth of 30-90 cm. The maximum duration of the snow period is around six months, *i.e.* from late October until mid-April. During winter, periods of severe frost (below -20ºC) alternate with thaws lasting for some weeks.

In Paazierre Forest, the studies were conducted in its three parts. The eastern part is a forested terrain in the upper reaches of the Lovats' river (hereafter the Lovats' terrain, Map 2.2), situated in the Haradok district in the Vitebsk region, *e.g.* 55º46'N, 30º15'E. Lovats' terrain has mostly hilly relief originating from the last glaciation (Matvieiev *et al.*, 1988). The surface ground deposits contain a high amount of clay, resulting in a good water supply and abundant trace elements, producing a rich soil. Plant communities have high species diversity and productivity, resulting in heterogeneous habitats. In general, the Lovats' terrain contains habitats with a high carrying capacity for herbivores and, in turn, for their predators. Premature coniferous

stands (32% of the area), mid-successional small-leaved forests (14%), and black alder swamp forests (16%) prevail. Among the coniferous stands, spruce-prevailed forest occurs the most. Also extended bogs overgrown largely with suppressed pines occur. Stream density in the Lovats' upper reaches is about 0.7 km/km^2, besides, there are small and medium-sized glacial lakes (0.3-2 km^2). Open grassy marshes occupy about 11% of the area and are common in the valleys of rivers and glacial lakes. Remote patches of open grassy marshes are mostly small and scattered. Man-made landscape elements (fields, hay meadows, villages, roads etc.) make up about 8% of the available habitats. Both agricultural lands and villages are getting deserted and natural habitats expand to the rural areas there, over time.

Map 2.1. Paazierre Forest (PF) and Naliboki Forest (NF) on map of Belarus

During the period 1990-2000, the following supplies of typical wolf preys were found. The elk population density in 1990-1991 was about 82 inds per 100 km^2; then it steadily declined with a minimum in 1994-1996, being one-tenth of those recorded in 1990 (more details in Sidorovich, 2011). After 1997, elk numbers grew, where in 2000 they reached 40-50% of the initial numbers; the elk population density was assessed as 39 inds per 100 km^2. In contrast, roe deer densities were low during 1990-1995, whereas they increased 5 to 10-fold until 2000, when the species population density was about 0.4 to 2 inds per one km^2. The wild boar, always a dominating species in the wild ungulate community, declined more than ten times from 1990 to 1996 and recovered in 1997-2000 to reach 60-80% of their initial densities. It was hard to estimate the wild boar population density, nevertheless, we may say that in 1990-1991 there were 0.5-3 wild boars per one km^2. The red deer was almost absent in the Lovat terrain. Concerning the beaver population density, it varied approximately between one and two inds per one km^2.

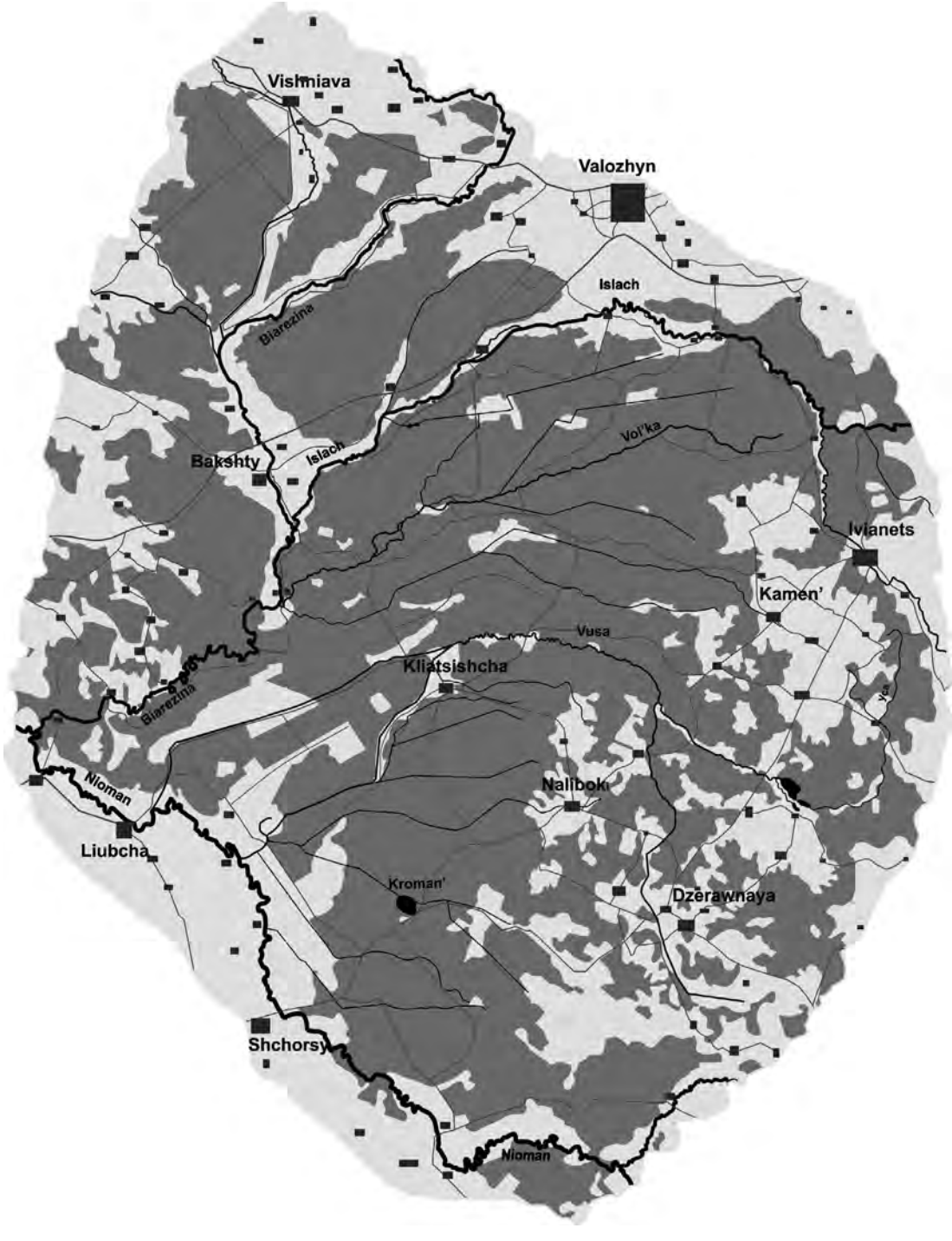
Before 1995, the Lovat terrain was entirely open for hunting during the cold season in the period of the mid-October-January

Map 2.2. Paazierre Forest on map of northern Belarus, locations of the Lovats' terrain (LT), Palata terrain (PT) and Krasny Bor terrain (KBT) in Paazierre Forest

for shooting of wild ungulates and till April for shooting of wolves. However, since 1995, one third of the area was transformed into a reserve for protection of vertebrate predators, and hunting of wolves was not allowed there anymore.

During the period 1990-2004 we carried out studies in the Lovat terrain on the wolf between-year population changes (number, population density and pack composition), the predator diets, food intake and impact on the prey populations. A lot of snow-tracking of wolves was fulfilled to learn their hunting manners and efficiency. We discovered 33 wolf dens with pups (in 23 litters we could count pups precisely), and the majority of pups were marked with clipping of one finger, then their locations and other characteristics (*e.g.* taking part in breeding, belonging to a given pack *etc.*) were traced by means of recognizing their specific footprints. Numerous snowtracking of a particular wolf pack and regular checking of the distributions of the marked individuals indicated their home ranges.

Within the Paazierre Forest, another study area was chosen on sandy soil, which is characterized as an ecologically poor region. It can be described as a sand dune



Map 2.3. Map of Naliboki Forest and its rural-forest surroundings, central-western Belarus

massif in the central north of Paazierre Forest, in the upper reaches of the Palata river (hereafter the Palata terrain, Map 2.2), Polatsk district, Vitebsk region, *e.g.* 55º41'N, 29º27'E. Stream density of the Palata upper reaches is about 0.4 km/km^2, and also in this area there are many small and medium-sized glacial lakes. The surface ground deposits consist mostly of sand, with clay only occurring in the valleys of glacial lakes and rivers. The soils of the area are very barren with poor water supply. Thus, the woodland is fairly homogeneous and it is dominated by pines. Dry land pine stands have very poor ground vegetation, basically consisting of moss and lichen. Dry land pine stands comprise about 60% of the area and 19% of the area are occupied by raised bogs with suppressed pines. Consequently, the animal community is species-poor with low population biomass.

During the period of study, the prey supply for wolves in the Palata terrain was rather poor: 9 to 20 elks per 100 km^2; approximately 40 to 60 beavers per 100 km^2; rather low density of wild boars and roe deer; the red deer was absent.

The Palata terrain was a game area during the whole study period on wolves there, however, the hunting in this remote and ecologically poor area was actually not intensive.

In 1998-2003 in the Palata terrain we mainly checked possibilities of wolf denning in this ecologically poor area as well as we tried to learn the winter pattern of this territory usage by wolves.

The third and last terrain that was used for the study on wolves in Paazierre Forest is called Krasny Bor, situated in the Rasony and Vierkhniadzvinsk districts of the Vitebsk region (Map 2.2), *e.g.* 55º58'N, 28º22'E. The Krasny Bor terrain is densely forested and has both clay and sand topgrounds in different localities. In the conditions of a rugged relief of the Krasny Bor terrain, various habitats are represented in fairly small plots. Together with plenty of aquatic ecosystems, the variety of dry land and swamped biotopes create a diverse habitat mosaic in this terrain.

The topographic structure of the Krasny Bor terrain is as follows: two medium-sized rivers, namely Nishcha (in the east) and Svol'na (in the west), flow southwards at a distance of 6-15 km apart. There is a huge sand dune massif south-east of the large Lisna lake, but relief in other places has basically originated from fluvial-glacial sediments (eskers and kames) over moraine deposits. In the center of the Krasny Bor terrain, there is an extended raised bog named Vialiki Mokh, which has an area of

about 17 km^2. In the peripheral parts of the bog, eight fairly small glacial lakes are situated.

In Krasny Bor coniferous stands prevail on dry lands. In the early 2000s, dry land pine stands covered about 26% of the area; spruce-dominated forest 24%; succession small-leaved deciduous forest -13%; raised bogs were present on 9% of the Krasny Bor terrain, black alder swamp on 5%, clear-cut up to 7 years old covered 7%, open grassy marshes about 8% and aquatic ecosystems 5%. In the 2010s, intensification of logging gave markedly higher portions of recent clearcuts and led to a decline of the area occupied by coniferous forest elder than 60 years.

In the period 1985-2014, we investigated the wolf population changes in the Krasny Bor terrain in connection with the dramatic increase of the rate of wolf persecution by humans; much data on the intensity of food intake by wolves, age and sex composition of the species population were gained. Also, snowtracking of wolves on the questions of their foraging and relationship with lynxes was conducted for many times and hundreds of kilometers.

During our quite long period of study in the Krasny Bor terrain, the prey supply for wolves varied greatly. In the 2000s, the local hunting wardens of the well-established game husbandry made rather exact census of wild ungulates and beavers. Thus, there are a lot of data to characterize the wolf food base in Krasny Bor. However, the prey stock description may be too long and complicated, and actually there is no need to describe all the changes in detail. The wolf food base in the 1980s and early 1990s was moderate; there were many wild boars, beavers and elks (at least, one elk per one km^2), but the red deer was absent, and the roe deer was rare. Later in the 1990s and the beginning of 2000s, the wolf food base was scarce. Afterwards, it increased greatly up to about 50-70 elks per 100 km^2 and high number of wild boars (5 to 30 inds per one km^2) and red deer (up to about 40 , mean 3 to 5 inds per one km^2).

Before 1997, the Krasny Bor terrain was entirely open for hunting during a part of the cold season, but since 1997 in half of the area the game husbandry was transformed into a reserve for landscape protection, and hunting of wolves was slightly limited there.

In Krasny Bor as well as in the other parts of Paazierre Forest (not only the Lovat terrain and Palata terrain) since 1985 we tried to obtain as much as possible information on wolf fecundity in relation to the species

population trend, first of all, the population density decline in effect of persecution by human.

2.2 Naliboki Forest

Naliboki Forest was another a wide-ranging forested terrain (Map 2.3), where a lot of studies on wolves particularly on the species reproduction, food niche and wolf-lynx interference were carried out. Naliboki Forest is in the central-western part of Belarus (Map 2.1), the districts of Valozhyn, Iwie, Navahradak and Stawptsy of the Miensk or Harodnja regions, *e.g.* 53°55'N, 26°20'E. In Naliboki Forest the forest habitats give about 88%. Similarly to Paazierre Forest, coniferous and small-leaved deciduous trees predominate in Naliboki Forest, too. Various pine stands (40% of the forested area) and black alder swamps (27%) prevail. Among pine forest, both dry land and slightly swamped ones are common. Dry land mixed coniferous-deciduous forest, spruce forest, swamped birch forest and broad-leaved stands are also common there. Only about 7% of the forested area look like a mature forest older than 80-100 years, which also includes 200-400-year-old deciduous old-growth presented in 2% of the forested area. River density comprises about 0.9 km/km^2, but many of the small rivers were canalized in the 1960s-1980s. Due to the terrain-wide draining there are many canals – approximately 2 to 9 km/km^2. Canals have forested bank sides and the majority of them were densely populated by beavers that created many small ponds. The habitat variety and ecological structure of Naliboki Forest was described in detail in the terrain monograph (Sidorovich, 2016).

The climate of Naliboki Forest is slightly milder then in Paazierre Forest, and was also described in detail in the terrain monograph (Sidorovich, 2016).

In the period of 1999-2017 we investigated the local wolf population in a rather detailed way in Naliboki Forest. Huge amount of dietary studies on a pack level in a seasonal dynamic of habitats were accomplished. In many cases we analyzed separately the summer diets of pups and their parents. Also the wolf between-year population changes (number, population density and pack composition) were investigated. During numerous snowtracking efforts of particular wolf packs we learned their home ranges. However, the main studies on wolves in Naliboki Forest we carried out in relation to the species reproduction; 44 wolf dens with pups were found (only in 39 litters we could count pups precisely) and their life story was

studied as long as possible (for 26 litters we assessed survival). Until 2004, the pups discovered were marked with clipping of one finger. The research question concerning the competition of wolves with lynxes, especially the species interference, was studied in an intensive way.

During this period the following supply of preys for wolves was found (Sidorovich, 2011, 2016). During the long period 1999-2012 the supply of preys was very rich (more details in Sidorovich, 2011). The most common prey species was the beaver (511-1547, mean 847 inds/100 km^2), followed by the roe deer (213-622, mean 398 inds/100 km^2) and the wild boar (139-376, mean 234 inds/100 km^2). Population density of the elk and red deer was lower, but these prey species were still common – on average 58 and 99 inds/100 km^2, respectively. It appeared that approximately each 100 km^2 there were 1636 individuals of the main prey species or about 16 per one km^2. The average prey species biomass was about 1308 kg per one km^2.

During February-July of 2013, the supply of wolf preys declined greatly. Extremely long-lasting and abnormally snowy winter affected the wild boar and roe deer population dramatically. Additionally, in June and July wild boars were affected by a severe disease. The prey census that was conducted afterwards (in October 2013) gave the following results: beaver (645 inds/100 km^2), roe deer (29 inds/100 km^2), wild boar (27 inds/100 km^2), elk (52 inds/100 km^2) and red deer (107 inds/100 km^2). So, the population number of roe deer decreased 14 fold and that of wild boars decreased 9 fold. Additionally, the heavier predation of wolves on beavers, seemed to have led to the clear reduction in this species population: the beaver population density decreased for 24%. Then during the hot and dry summer of 2018 the beaver population in Naliboki Forest was redused approximately a half again.

During the last years (2016-2019) other changes in the local vertebrate community that are essential for reproduction in wolves happened in Naliboki Forest. The first change in the local vertebrate community is that during the last years, Naliboki Forest appeared to be densely populated by lynxes (since 2015 more than 40 inds, in 2018 more than 80 inds). In 2018, the lynx population density in Naliboki Forest constituted about 5 inds per 100 km^2. This rather high density of lynxes was plausibly determined by very favourable habitat conditions in Naliboki Forest. There are still many old forest patches and simultaneously

many clearcuts, whereas most of the numerous drainage canals are blocked by beaver dams. All such habitats are densely inhabited by roe deer, red deer, beavers, hares, grouses and ducks, and these animals are suitable prey for lynxes.

The second change is that during 2015-2018 the number of other vertebrate animals such as bison, elk and stags (*i.e.* relatively big red deer males) increased markedly in Naliboki Forest. These animals are usually aggressive towards wolf pups and wolf denning in general. In the spring of 2018, there were not fewer than 100 bison in Naliboki Forest, and approximately 20-50 stags per 100 km² and 40-80 elks per 100 km².

Also, during the last decade, up to 12 brown bears (mostly adult males) appeared in Naliboki Forest, and that plausibly has a negative impact on wolf denning as well.

During our study period, in about half of Naliboki Forest, there was some kind of reserve status adjusted, and hunting was limited in the reserve, but these limitations were not so much valid for wolves. In 2005, half of the Naliboki Forest was recognized as a landscape reserve. Since that year on, and even a few years before, hunting on wolves in the reserve was more or less limited, and, at least, during half of these years no wolves were legally killed in the reserve.

After this text in relation to the study areas that were used to investigate the local populations of wolves, a photo-presentation about the habitats in Paazierre Forest and Naliboki Forest is given. The following two categories of habitats are shown: the landscape-prevailed ones and the wolf-important ones. Among the wolf-important habitats, special attention was paid to the variety of denning habitats and those essential for further pup raising after the initial denning period.

(5→) *Forested road rarely used by people and twilight is wolf habitat and wolf activity time. Naliboki Forest, Valozhyn district, Miensk region.*

(6↑) *Small river of Stsiudzionien'kaja. Paazierre Forest, the Rasony district, the Vitebsk region.*

(7↓) *Wolves are crossing small river by the fallen tree.*

(8, 9↑↓) *Wolves are walking on ice along drainage canals that are particularly plenty in Naliboki Forest.*

(10↑) *Edge of open marshland in Naliboki Forest, the Valozhyn district, the Miensk region.*

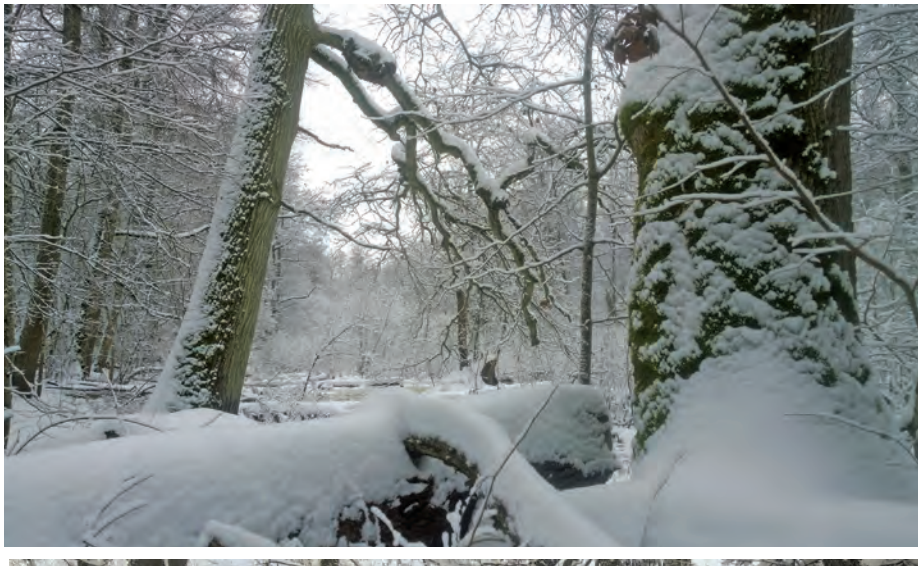
(11←) *Reed open marshland in Paazierre Forest, the Rasony district, the Vitebsk region.*

(12↑) *Large raised bog with suppressed pine stand of Vialiki Mokh. Paazierre Forest, the Rasony district, the Vitebsk region.*

(13↓) *Marshy valleys of glacial lake of Nitsiattsy with forested island. Paazierre Forest, the Rasony district, the Vitebsk region at the border with Russia, Pskov region, Siebiezh district.*

(14, 15↑↓) *Spruce-prevailed tree stand is common habitat in Naliboki Forest, the Navahradak district, the Harodnja region (above photo) and the Valozhyn district, the Miensk region (below photo). Spruce forest is usually well-sheltered, and that attracts wolves in this habitat type.*

(16→) *Spruce-prevailed forest is common habitat in Paazierre Forest, the Haradok district, the Vitebsk region.*



(17↑←) *Forested edge of river valley in Naliboki Forest. There are many oaks in the tree stand. The Navahradak district, the Harodnja region.*

(18, 19↑) *Valley (at the left) and non-valley broadleaved deciduous tree stands in Naliboki Forest. The Navahradak district, the Harodnja region.*

(20←) *Mixed forest that consists of spruces and black alders covers a considerable part of lowland Naliboki Forest. There are more or fewer spruces in such a forest and treefalls are common there. The Valozhyn district, the Miensk region.*

(21→) *Recent clearcut among spruce forest in flat land in Naliboki Forest. The Navahradak district, the Harodnja region.*

(22↓) *Recent clearcut among pine stand on sand dunes is a common habitat in many areas of Paazierre Forest, the Vierkhniadzvinsk district, the Vitebsk region.*

(23, 24↑↓) *Abandoned and having few inhabitants hamlets and homesteads are an essential part of the landscape in Naliboki Forest. The Valozhyn district, the Miensk region (above) and the Iwie district, the Harodnja region.*

(25←) *Forest roads are very important habitats of wolves in Belarus year-round. Wolves often hunt, while patrolling roads, they use roads for territorial marking and fast moving from one place to another one. During mating season adult wolves start marking many new sites even in the areas, where the species was absent before. Usually the most of marking sites that frequently used in the snowless period being under deep snow are forgotten by wolves, whereas many new ones, for instance, on prominent snow heaps appear. In this period marking by wolves are carried out mainly by urinating, while scratching is not applied much anymore. Naliboki Forest, the Valozhyn district, the Miensk region.*

(26←↑) *Pair of wolves at road marking point.*

(27↑) *Urinating by wolf breeding group. The female's urine contains blood that indicates proestrus phase in the female wolf and oestrus approximately in 7–10 days. This feature is very useful to get know, where there may be wolf breeding groups.*

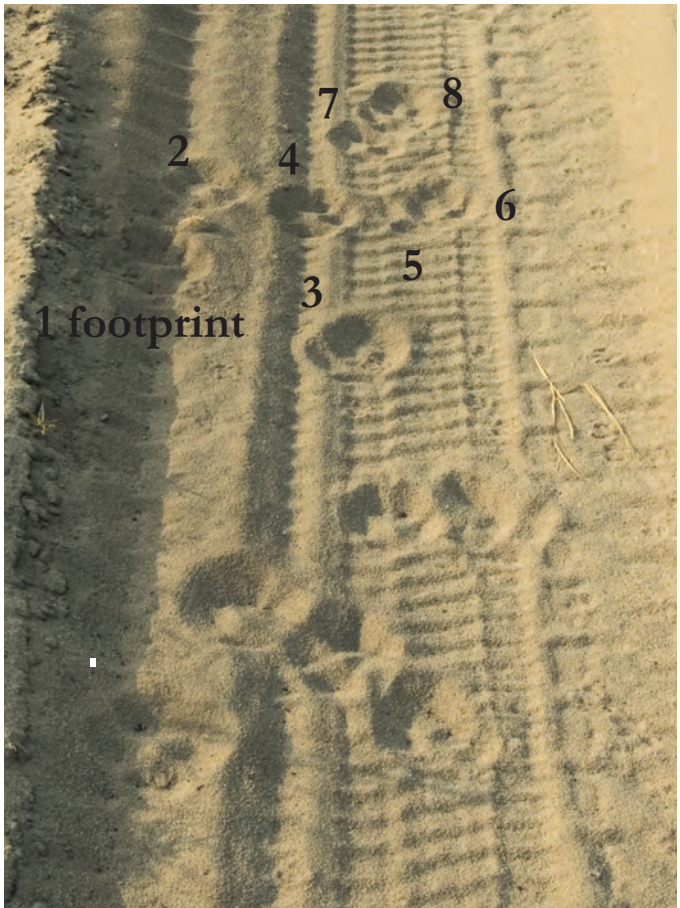
(28←) *Wolf marking point in mating season. According to snowtracking data, during this busy time wolf adults mark many (sixty and more) times per twenty-four hours. Some of the marking points may be marked by the same wolf for several times per day.*

(29←) *Split trails of pack of five wolves. In such a situation you can count the number of individuals in a pack.*
According to snowtracking data, roads take approximately 60–80% of wolf walking. With such roads it is much easier for wolves to control their territory by traveling fast enough. Naliboki Forest, the Valozhyn district, the Miensk region.

(30↑) *Trail fragment of pack of four wolves. In such a situation you can count the number of individuals in a pack.*

(31←) *Scratch marking by big male wolf at forest road.*

(32-35) *Wolf territorial marks and wolves at marking.*



(36↑) *Scratch marking by wolves on roads. Naliboki Forest, the Navahradak district, the Harodnja region.*

(37←) *Four wolf trails on road. If wolves walked not enough splitted, i.e. as you see in the right photo, to find out the number of wolves passed, you need to count number of footprints in one group and then divide the number by two (i.e. there are both fore and hind footprints of each wolf that passed here).*

(38↓) *Footprints of wolf pups.*

(39-42) *Small sand dunes on glade are frequently used by wolf family with pups for grooming. Naliboki Forest, the Iwje district, the Harodnja region.*

(43-46) *Moraine hills covered by coniferous mixed forest or mostly spruce forest that interspersed with smaller or larger grassy openings is a typical terrain in Paazierre Forest. The Haradok district, the Vitebsk region.*

(47↑) *Pair of wolves in April before denning. The last 10-20 days before parturition wolf breeders stay locally and move usually not much. Only the founding male may go for hunting quite faraway leaving his heavily pregnant female alone.*

(48, 49↓→) *Wolf den in kind of a covered cavity under roots of big spruce and black alder (almost like a burrow).*

(50) *Denning habitat of wolves. Naliboki Forest, the Valozhyn district, the Miensk region.*

(51) *Wolf pups 5-7 days old in cavity-den under uprooted spruce.*

(52) *Entrance in the den.*

(53-55←↓) *Wolf denning sites in spruce forest with a lot of treefalls. Naliboki Forest, the Valozhyn district, the Miensk region.*

(56↑) *Irina Rotenko is searching for wolf den. Naliboki Forest, the Valozhyn district, the Miensk region, 2011.*

(57↑) *The pups one day old on the den.*

(58←) *Vadim Sidorovich in the moment of just finding wolf den with pups. The pups are one day old. Naliboki Forest, the Valozhyn district, the Miensk region, 2010. Photo by Klaus Feichtenberger.*

(59↑) *Wolf denning site in treefall among spruce forest. Naliboki Forest, the Valozhyn district, the Miensk region.*

(60, 61←↓) *Wolf dens with one and five pups. The dens were situated at root plates of uprooted spruces.*

(62↓) *Vadim Sidorovich at wolf den with only one pup. The den was situated among fallen spruces overgrown with young spruces. Naliboki Forest, the Valozhyn district, the Miensk region, 2012.*

(63↑) *Wolf denning site under windfall of birch forest. Paazierre Forest, the Shumilina district, the Vitebsk region.*

(64→) *Wolf denning place under windfall of birch forest. Naliboki Forest, the Valozhyn district, the Miensk region.*

(65↑) *Dry place under an old spruce, where a breeding female wolf gave birth.*

(66←) *Open couch-den of wolves in kind of a dimple to prevent creeping of the pups. Such a den is more typical for wolves during the first 10–15 days of the pups.*

(67←↓) *Open den of wolves in kind of a larger couch that is more typical for slightly older pups of 15-25 days old.*

(68↓) *Wolf den in a cavity under roots of big spruce with nine pups.*

(69-73 ←↑↓) *Eleven wolf pups about ten days old in self-dug cavity-den under rotten stamp with peat soil.The active and previous dens are shown above. Vadim Sidorovich is working with the pups: identifying a sex of the pups, takling hair samples for genetic analysis etc. Naliboki Forest, the Stauptsy district, the Miensk region.*

(74↑) *Suitable denning place of wolves in clearcut of spruce forest with some treefall at the edge and early reforestation by spruces mostly. Naliboki Forest, the Valozhyn district, the Miensk region.*

(75-80←) *The variety of wolf dens that were found in young spruce reforestation.*

(81→) *This pup about 20-25 days old was relocated aside from the den by one of the parents, when we were nearby the den.*

(82←) *Suitable denning habitat of wolves in black alder swamp. Wolf breeders, while denning, quite usually create a cavity-den in rotten wood material between the root system of old black alders. Naliboki Forest, the Navahradak district, the Harodnja region.*

(83↓) *Black alder swamp is so common in Naliboki Forest and also present in Paazierre Forest. The Iwje district, the Harodnja region.*

(84↑) *Medium-sized river of Biarezina in Naliboki Forest with broadleaved deciduous old forest in the valley. The Navahradak district, the Harodnja region.*

(85, 86↓←) *Non-valley broad-leaved deciduous oldgrowth in Naliboki Forest is very rich hunting habitats for wolves, while they are breeding. The Navahradak district, the Harodnja region.*

(87) *Small glacial lake of Niemtsava in Paazierre Forest. There are many glacial lakes in Paazierre Forest, and their shores are important hunting habitats of breeding wolves. The Haradok district, the Vitebsk region.*

(88) *Small glacial lake of Lavatsets. Paazierre Forest, the Haradok district, the Vitebsk region.*

(89) *Medium-sized glacial lake of Tsiosta with islands. Paazierre Forest, the Haradok district, the Vitebsk region.*

(90, 91↑↓) *Large raised bog. It is common but relatively poor hunting habitat for wolves, but denning area of local wolves may be situated just there. Paazierre Forest, the Haradok district, the Vitebsk region.*

(92, 93←↓) *Numerous beaver ponds in both Naliboki Forest and Paazierre Forest are favorable habitats for wild ungulates, which and beavers themselves attract wolves to hunt there. The above photo was taken in Naliboki Forest, the Iwje district, the Harodnia region; and the below one in Paazierre Forest, the Haradok district, the Vitebsk region.*

(94, 95) *Drainage canals are ver common habitat type in Naliboki Forest. Usually the canals are inundated with damming by beavers. The Navahradak district, the Harodnja region (above photo); the Valozhyn district, the Miensk region (below photo).*

(96↑) *Pine stand on sand dunes is wolf habitat type with very low prey supply. Nevertheless, mainly absence of people and, perhaps, low mosquitos abundance in May-June attract wolves for denning just in these habitats. There they mostly den at boggy pine stands with dense shrub cover, which provide enough sheltering for pups. Pine stands are common in both Paazierre Forest and Naliboki Forest. Naliboki Forest, the Stawptsy districts, the Miensk region.*

(97←) *Boggy pine stand with dense shrub cover. Naliboki Forest, the Iwje district, the Harodnja region.*

(98↑) *Pine stands on sand soil are widely spread poor quality habitats in both Naliboki Forest and Paazierre Forest. On the photo it is pine stand in Naliboki Forest. The Iwje district, the Harodnja region.*

(99, 100↓) *Wolf cavity-den in pine stand under root plate of inclined pine tree. In such habitat a wolf den is hidden by large space, where nothing to do for human and wild ungulates in May-June.*

(101←) *Wolf burrow-dens in young birch-spruce plantation. Initially that was red fox earth, and wolf breeders enlarged the burrow. Naliboki Forest, the Navahradak district, the Harodnja region.*

(102↑) *Pup chamber in wolf burrow-den.*

(103 ↓) *Passage to the pup chamber in wolf burrow-den.*

(104, 105 ↑↓) *Eleven pups are inside of the enlarged red fox earth, i.e. seven pups above in the pup chamber and below you see four more pups, which hided in the narrower red fox passage.*

(106-108) *Wolf burrow-den in pine stand on sand dunes; wolf litter in such a den; and mother wolf is enlarging a burrow for her litter in Naliboki Forest.*

(109, 110↑) *Wolf couch-den under small spruce in pine stand. Naliboki Forest, the Stauptsy district, the Miensk region.*

(111, 112↑→) *Wolf cavity-dens in pine-spruce stands. Naliboki Forest, the Stauptsy district, the Miensk region.*

(113→) *Wolf litter on grooming spot within the family housing place at canal among pine-spruce stand. Naliboki Forest, the Valozhyn district, the Miensk region.*

(114, 115↑↓) *Wolf litter on grooming spot within the family housing place among young spruce-birch forest. Naliboki Forest, the Iwie district, the Harodnja region.*

(116↑) *Small river of Vol'ka in Naliboki Forest and its open valley wetlands favour wolves for successful hunting. The Iwje district, the Harodnja region.*

(117←) *Open marshy grassland in the Biarezina valley. Naliboki Forest, the Iwje district, the Harodnja region.*

(118↑) *Open sedge marsh with forested islands. Naliboki Forest, the Valozhyn district, the Miensk region.*

(119↓) *Open reed-sedge marsh in the former valley of the Vusa river. Naliboki Forest, the Navahradak district, the Harodnja region.*

(120↑) *If in a forested terrain there are large meadows on drained lands usually, such a meadow may be used by breeding wolves as a denning habitat, when the height of grass stand is about 40 cm and taller. There pups may be placed either nearby the opening center or at its edge at the border with forest. Closely located terrain roads are not avoided by such wolf families, if the grass thicket is sheltered enough. There wolf parents evidently prefer to place pups at drainage canals, if they are present among such openings. Sometimes, there wolf parents dig burrows preferably in canal banks or on relatively higher plot with sand layer. The evident benefit of such a denning habitat is following: rather low abundance of mosquitoes, easy watching of surroundings, well-sheltered environments for pups and quite often for parents as well. During too rainy weather, pups may be temporarily replaced in neighboring forest. If nobody disturbs such a wolf family, they may stay there until mid-October. This photo was taken in Naliboki Forest, the Navahradak district, the Harodnja region.*

(121) *Wolf burrow in grassy opening that was dug on relatively higher plot with sand layer.*

(122, 123↑↓) *Grass trampled by wolf family.*

(125) *Mother wolf in grassland.*

(124) *Wolf denning plot in grassy opening. Naliboki Forest, the Valozhyn district, the Miensk region.*

(126) *Mother wolf coming to road from the open den site among-grassy opening.*

(127↑) *Red deer groups on dry land meadows in early spring. Naliboki Forest, the Valozhyn district, the Miensk region.*

(128←) *Harvesting of grass on drained lands. Naliboki Forest, the Stawptsy district, the Miensk region.*

(129→↑) *Large herd of caws on meadow on drained lands. The caw herd belongs to collective farm. Naliboki Forest, the Valozhyn district, the Miensk region.*

(130→) *Some private cattle on meadow. Naliboki Forest, the Valozhyn district, the Miensk region.*

(131↑) *Well-sheltered young spruce thicket, where parent wolves place pups for temporal stay during summer and early autumn. Naliboki Forest, the Valozhyn district, the Miensk region.*

(132←) *Young wolves on stay in treefall as well-sheltered habitat.*

(133-138→) *Well-sheltered spots, where parent wolves may leave pups for temporal stay during summer and early autumn. Naliboki Forest, the Stawptsy district, the Miensk region and the Navahradak district, Harodnja region.*

(139, 140↑↓) *Abandoned peatery with pools, drainage canals, peat mounds and accumulation of stumps. This is relevant habitat for wolves, and quite often breeding wolves den there. Naliboki Forest, the Stawptsy district, the Miensk region.*

(141→) *Peat mound among abandoned peatory that was used by wolves for resting and watching a lot. Sometimes wolf breeders dig burrow in such a peat mound. It is for temporal placing of small pups and for sheltering of pups during rainy weather. Naliboki Forest, the Valozhyn district, the Miensk region.*

(142↓) *Accumulation of stumps in abandoned peatery is a relevant place fo wolf denning. Naliboki Forest, the Stawptsy district, the Miensk region.*

(143↑) *Abandoned peatery with pools, drainage canals and peat mounds. Paazierre Forest, Shumilina district, Vitebsk region.*

(144-146↑→) *Wolf cavity-den in abandoned peatery. The wolf pups are about fifteen days old.*

(147-149↑←) *Wolf den in kind of a burrow dug by parents in peat mound that situated in abandoned peatery. Vadim Sidorovich is checking the pups, which are only one day old. Paazierre Forest, Shumilina district, Vitebsk region, 2001.*

Chapter 3. Methods

In this chapter we describe the variety of basic methods that were applied in the given studies on wolves in Belarus. These methods were categorized into eleven items: (1) method of wolf census and approach to estimate the species population density, (2) snowtracking of wolves and identification of wolf tracks, (3) collecting information from the individual wolves that were marked with a clipped finger, (4) wolf pup searching and study on wolf denning behavior, (5) estimation of wolf fertility parameters, (6) investigation of wolf pack composition, (7) study on the interference between wolves and lynxes, (8) gathering of scats of wolf pups and parents, analysis of the scats in order to reconstruct the pup and parent diets, (9) determination of wolf age, (10) estimation of the population density of the main prey species (11) statistical methods.

3.1. Method of wolf census and approach to estimate the species population density

Basing on track information, wolves may be counted in the first half of winter (mid November–mid January). The area of wolf census needs to be larger than 1000 km^2. In suitable snow conditions (not deep and loose snow cover, 1–4 days after the last snowfall) the whole network of terrain roads should be inspected with a vehicle during a short period of 2–5 days.

In Belarus as well as in many other regions of Europe the terrain road network is dense enough even in forested areas, and, so, in such areas all wolf packs are likely to be registered by their track trails that crossed the roads or when they walked along the roads. When you face a wolf trail (looks like of either lone individual or pack), you need to follow the trail in order to find out the number of individuals walking there. You may learn that in the places, where the joint trail splits (see Photos 29, 30 and 37). In November and till mid-December number of pups can be still counted due to their still markedly smaller footprints in comparison with footprints of adults. In some packs one or several adult males may have outstandingly big fore footprints or one of the wolves may be with an abnormal foot such as there is no one finger or claw *etc.* Together with counted number of individuals in each registered track trails of wolf pack, all other specific track information (*i.e.* number of pups in a pack, presence of individuals with outstanding footprints) should be mapped. These information will provide all that it is needed to get know about the local wolf population in the area of the species cen-

sus: the number of wolf packs, and number of individuals in each pack in census area, the composition specificity of the registered wolf packs. To make sure of the robustness of the gained result, such wolf census must be repeated in one or two weeks.

In Naliboki Forest every year census of wolves was carried out by our own efforts with the above-described method. In 2014-2017 in Naliboki Forest camera traps were largely applied to get extra information.

In Paazierre Forest and some other areas we used estimates of number and population density of wolves, which were produced by wardens of game husbandries or nature guards of protected areas. In these cases usually we checked the veracity of such an information. In the cases of overestimation, we corrected the estimates by decreasing them. Indeed, sometimes, the neighboring game husbandries counted twice the same wolf pack, which partly lived in the two areas. Therefore, to correct the information on wolf number (repetition) it was calculated a potential maximum of wolf number in the area by means of two parameters: plausible minimal home range of a wolf pack in Belarus is 250-300 km^2 and average number of individuals in a pack is 5-6. If the estimated wolf number in a particular region was reported higher than the potential maximum that we calculated for the area, in this case we accepted this calculated by us maximal value as more precise estimate.

We calculated wolf population density as an average number of wolves, which live per 100 km^2 of the wolf census area, *i.e.* we simply divided the number of wolves that were censused in the area by the number of km^2 in the area and then it was multiplied by 100. So as highly mobile mammals, wolves usually live in a large territory of 300-400 km^2, the census area of wolf covers 1000 to 3000 km^2.

We consider the wolf population density of 2 and more individuals per 100 km^2 as a high one; 0.5 to 2 – medium; less 0.5 – low. We distinguish two kinds of density values in the wolf population in Belarus. First we consider a local population density of wolves. For instance, in Naliboki Forest there is a reserve with no hunting, and density of wolves in this forest massif is usually thus higher than outside in the agriculture-forest mosaic landscape.

In this case, this local population of wolves is functionally a part of a much larger wolf population. So, in the analysis we also use the wolf density in the whole population for a much larger terrain. In Belarus, such a terrain includes not only vast forest, but also continuous rural areas and agriculture-

forest mosaics, where wolves are heavily persecuted by hunters each year.

Other rural landscapes devoid of forests and rural-forest mosaic are also suitable wolf habitats, because the numbers of wolves there were registered to be quite high in some historical periods.

In spite of the fact that local forested patches can include marked high densities of wolves, we can therefore see that the whole wolf population is relatively low for most of the years.

We assume that just the whole population-wide density of wolves mainly acts as a factor in intrinsic regulation, and just this density value should be taken in to account, first of all, when the population density is considered as a possible significant factor of the population dynamics.

On the other hand, such a locally registered density of wolves is, perhaps, less essential for trends in reproduction biology of wolves. It is worthwhile to notice that a rough usage of not a right population density value may lead to an artefact in understanding of a role of density in a reproduction trend.

Also, an important question is when the density of wolves is assessed. Indeed, in Belarus each year extermination of wolves on game areas leads to already unsaturated wolf population even in the post-reproductive period. Moreover, each year before the wolf mating season a half of wolves are killed by hunters. More precisely it is going on in Belarus like following. While analysing hunting bags, approximately 90% or even higher portion of the killed wolves were hunted every year by hunters in the period of the mid-October till the mid-April. Usually, that happens in two steps: 50-60% of the killed wolves were hunted from mid October to the end of February and 30-40% during the reproduction period in March-April.

Thus, just after the reproduction, before the main harvesting of wolves, their density may have medium or even high values, but afterwards it may be low. We assume that in the breeding aspect just the species density before mating season is a crucial, and just such density value acts as a factor of a breeding rate. So, in Belarus, while mating, wolves are usually already in the conditions of a rarefied population with much vacant habitat carrying capacity. Such a situation with low density of wolves in the whole population may lead to the population reaction directing to breeding intensification despite of locally wolf density may be medium or high.

3.2. Snowtracking of wolves and identification of wolf tracks

Since 1985 altogether in Paazierre Forest and Naliboki Forest, wolves were snowtracked slightly more than 2200 km. Generally, wolves were snowtracked for several aims. The first, snowtracking seems to be the best way to investigate winter habitat use by wolves, because winter is the harshest seasonal period that determines the species survival rate a lot. Snowtracking of wolves shows in which habitats wolves hunt, where they rest, how often they use roads and visit human settlements *etc.* The second, efficiency of foraging and hunting manners can be well studied by snowtracking. The third purpose was to get an extra information about food intake by wolves. The fourth, participating of pups in the pack hunting may be checked only, while snowtracking such a pack having pups. The fifth aim was estimating of home ranges of wolves. Manifold snowtracking of the same pack with mapping of all their trails may provide quite correct data on home range size and structure. The sixth, territorial marking, intraspecific aggressive behavior and interference with other species *e.g.* the lynx, red fox and raccoon dog are worthwhile to check having snowtracking as one of the methods to investigate the questions. While snowtracking, there may be recorded the habitats passed through, movement distance in particular habitat types, details of foraging, prey consumption, resting *etc.*

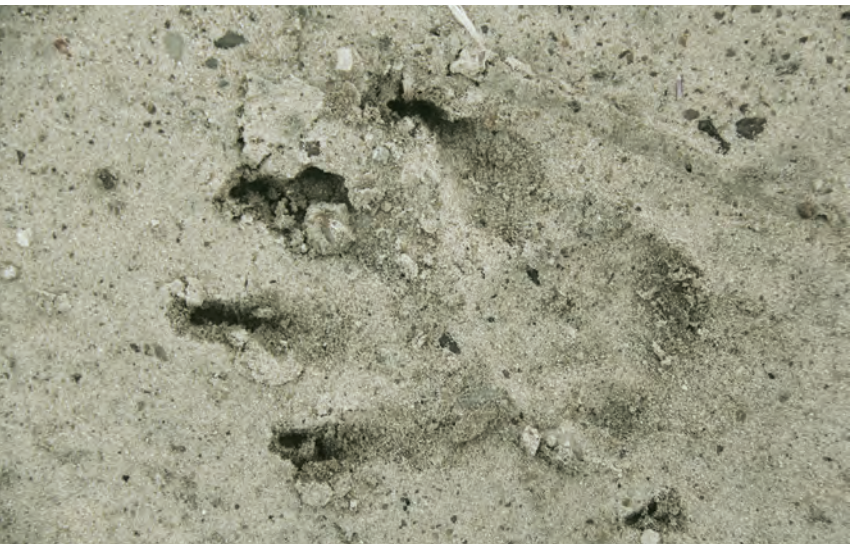
As the main focus of this book is reproduction biology in wolves, snowtracking data were here applied mainly for the questions of pup life in winter, first of all, their taking part in the pack movement, hunting and territorial marking. Footprints of pups of the year were recognized by either their smaller size in November and till mid-December or later with the marks of a clipped finger.

While snowtracking wolves in mating season and before, we were interested to find signs of proestrus in females (Kreeger, 2003), *i.e.* urination with bloody discharge (see Photo 27), what means that the female will get oestrus in 7-10 days. Also, we look for copulation spots. Usually it is a plot of 7-12 meters in diameter densely trampled by wolves with some secretion like urine, but without food remains.

Sometimes, it may be hard to differentiate tracks of the wolf and large domestic dog. Usually wolf footprints are bigger than those of dogs. Footprints left by wolves on a thin snow cover or loose ground are 8–13 cm long and 6–9 cm wide, whereas in the conditions of a loose snow cover these dimensions may be slightly higher. Prints of wolf digital pads are symmetric and oval, whereas in dogs they are frequently wider in rear part than in the front part.

(150) *Hind (at the left) and fore (at the right) footprints of wolf.*

(151) *Fore footprint of wolf.*



(152-154↑↓→) *Footprints of dog.*

(155↑) *Trotting track trails of two wolf-dog hybrids,*

(157↑) *Fore footprints of wolf, when it stopped.*

(156↓) *Trotting track trail of seven wolves. Every next wolf stepped the footprnts of the previous wolf.*

(158↓) *Trotting track trails of three wolves.*

Male wolf has wider footprints than those of female wolf. Ratio between length and width comprises about 1.3 in footprints of male wolves, and approximately 1.5 in those of female wolves. In wolf footprints all digital pads look more massive than those of dogs in relation to the interdigital pad, even of large dogs, and the two central digital pads in wolf footprints are mostly placed in front of the lateral digital pads. However, in a big male wolf the later feature is not pronounced, and this may be used for rough distinguishing of males and females among adult wolves by their fore footprints. The central digital pads are also placed tighter to each other in wolf footprints than those of stray dogs.

However, these observations are not totally reliable. Nowadays, some big dogs have big paws and rather massive digital pads like those of wolves.

Therefore, the two other below-following distinguishing features of wolf and dog tracks are crucial to make a decision to which species (wolf or dog) tracks belong.

These features originated from much trained paws of wolf as a hard walker as well the species energetically economizing walking pattern. In comparison with dog, wolf paw facing with the same substratum leaves more symmetric print of a rather strong foot. In the case of much weaker paw of dogs their footprints consist of pads that slightly distorted and slipped in different sides as well as dog's claw marks printed sideward often, and, so, dog's footprints look more asymmetric. Concerning wolf track trail, it is evidently more regular; stride of a wolf trail is markedly longer (60–70 cm versus 30–40 cm in dogs). Also, double footprints (superposed or in twos) of wolves are located strongly at a straight line for the most of trotting track trails. It is energetically economizing walking pattern. Dogs, while trotting, usually do not target by the hind paw in the fore footprint, and therefore their track trails consist of wavy footprint sequence with the markedly shorter stride.

3.3. Collecting information from the individual wolves that were marked with a clipped finger

Marking of wolf pups with clipping of one finger enriched the research results on nearly all questions of wolf population ecology that we dealt with. Concerning the topic of wolf reproduction biology, marking of wolf pups with finger clipping brought very interesting information on many pressing questions. Among them were the pup survival, distribution of yearlings during the next breeding of their parents, dispersal of subadults and how long they stay with parents as well as when they breed the first time *etc.*

Clipping of finger from wolf pups was carried out with dog-experienced vets. Before we started to mark wolf pups by such a method, we practiced it with pups of domestic dogs tracing their welfare. The experience suggested that the small wound recovered surprisingly fast, and there was no one case, when the dog pup with a clipped finger died from that.

While working with wolf pups handled, we had never used any repellent against mosquitos and never smoked. Otherwise, wolf parents could abandon the pups.

In 1997-2002 in the Lovat terrain, Paazierre Forest we marked by such a way pups from 26 wolf litters and afterwards we traced their distribution as long as it was possible. Similarly, in Naliboki Forest in 1999-2005 we marked pups from 9 litters, and then followed them with their special footprints. A total, by using this method in Paazerje Forest and Naliboki Forest, we succeeded to trace life story of 52 pups.

(159 *Recovered paw of wolf pup with clipped finger. The finger was clipped 9 days ago.*

(160) *Footprint of wolf with clipped finger.*

3.4. Wolf pup searching and study on wolf denning behavior

Long ago people searched for wolf pups and used to kill them for controlling wolf populations. We searched for wolf pups in order to investigate the species reproduction ecology and breeding behavior. The knowledge and skills were gained on the quite large materials: 75 dens with pups were found by us in Paazierre Forest and Naliboki Forest, Belarus. All those wolf pups found were left alive and in good health on the dens.

The method for searching of wolf den is worthwhile to be explained, because it has not been yet published with sufficient details

except of the mammal track guide by Sidorovich and Vorobej (2013). Of course, the publication of this method might help humans to continue to persecute wolf. There are, however, two main reasons to publish it.

First, while elaborating the management plan for the wolf population in Belarus in 2006-2008, we tried to substitute the practice of a bloody elimination of wolves by fladry method (*i.e.* with a chain of small red flags, hunt drive and shooters) with population control of the species by means of wolf pup searching and elimination of a part of the pups in each litter found. Afterwards, that was largely criticized by several experts from the western European countries, who expertized the draft of the wolf management plan in Belarus. Finally, this part was deleted from the plan by officials, who dealt with the wolf management plan. But we are still sure that it could be the most euthanasic approach in the wolf population control. Moreover, in our former native country of Great Lithuania in the 14th-18th centuries just wolf pup searchers provided successfully the main population control of the species.

Second, wolf pup searching is a very fruitful method to study on wolf reproduction and together with marking of pups with finger clipping it can give to a wolf researcher even more interesting information than telemetry. As to ethical aspect of clipping finger in pups, being experienced in both, we would like to say that telemetry with a cruel live-trapping and handling of wolves looks like far less ethical.

Before describing the way of searching for wolf pups, it is useful to give a number of knowledge, which provide necessary information background for such a groper. In the majority of such theses (or parts) a simplified and shortened information about wolves is given. In the result items of the book the information on the respective questions are represented more detailed and scientifically more precise.

Just in case it should be mentioned that in another region that has the distinctive environment conditions, perhaps, not all the below-considered features of the wolf breeding behavior and ecology are identical with those in Belarus. At the same time, undoubtedly the majority of the breeding characteristics of wolves in Belarus should be similar to those in many other regions of Europe.

The first thesis is very simple. That is when female wolves give birth and, respectively, it helps to find out, when it is reasonable to search for pups.

Usually in Belarus female wolves give birth in the period from the end of April till the end of May, and two third of litters appear

till 10th of May. Approximately each tenth litter appears around 20th of May. Sometimes, female wolf gives birth very early in the late March or early April.

Second thesis concerns denning habitat types of wolves in Belarus. Breeding wolves may den in thickets with many uprooted trees, especially with spruces (Photos 14, 15, 53, 56, 59); thickets in logging areas with a lot of tree remains and timber left-off (Photo 74); abandoned peatery with peat mounds left-off (Photos 139-143); and sand-dunes with young pines and small openings at the border with boggy habitats having dense ledum and bilberry shrubs (Photos 96-98, 106, 108). If in a forested terrain there are large meadows, such a meadow may be used by wolves as a denning habitat too (Photos 118-120, 124, 126), when the height of grass stand is about 40 cm and taller. When there are too many wolf-inimical animals such as lynx or wild ungulates, wolves shift their denning in coniferous stands almost without underforest and poor forest floor (Photos 50, 96, 98, 106, 108, 109, 111), where both lynxes and wild ungulates are not so common.

Third thesis, despite the wide-spread view that wolf pups should be located at a stream or another source of drinking water, actually it is very hard to apply this feature into practice to wolf pup searchers, at least, in Belarus and adjoining regions. Indeed, there are 0.4–0.7 km of watercourses per one km^2 on average. Moreover, in the areas, where draining was conducted, the stream density is several fold (locally more than tenfold) higher than it used to be. Additionally, usually there are numbers of other sources of drinking water. Thus, there is so much water for wolves to drink that the mentioned feature of plausible den location is not useful, because water is actually available everywhere. Only during severe summer drought (what actually became more usual during the last decades) precense of water source is getting an essential to place pups.

Fourth thesis, it is a pitfall approach, if a wolf pup searcher mostly inspects seemingly suitable places, even if somebody found wolf pups there before. Not only beginners, but sometimes wolf pup searchers, who are already more or less experienced with wolves, tend to choose such a wrong tactic. Merely when such a groper knows large terrain in all wolf-related details and has fairly large experience with wolf breeding there (*e.g.* there were found 15–20 dens with pups), denning behavior of the species may become predictable. Such an experienced wolf pup searcher may apply inspecting of the former denning areas of wolves more time. For others it will be inefficient.

(161) *Trail of a pregnant female wolf several days before giving birth. Footprints of the relatively heavy pregnant female are situated tortuously and the stride is markedly shorter than normally. Moreover, heavy pregnant female wolf produces noticeably deeper footprints on a relatively soft sand or muddy ground.*

Fifth thesis, the entire time wolf pup searcher should follow relevant tracks and other activity signs of breeding wolves. Otherwise, such a groper is ill-omened or will not be successful enough. In a great measure, looking for wolf pups is similar to tracking, but in a hard situation, when there is no snow. So, the only effective way of finding wolf pups is to learn reading of information that was hidden in tracks and other activity signs of wolves.

Sixth thesis, still it is a wrong way to search for wolf pups dealing with just a presence of many wolf tracks, if you are not sure that the tracks and other activity signs belong to breeders. A given pair (or larger group) of wolves, which looks like breeders, actually may be yearling wolves or older non-breeders. Moreover, during denning period yearlings are similarly to parent wolves stay in a small area of usually up to 30 km^2. This may embrangle wolf pup searchers. Such a mistake as well as any other mistakes in this complicated job is not trifling. The period, when it is possible to hand and investigate wolf pups, lasts 20–30 days only. So, even few days that were spent in vain in this busy period affect seriously the final results of the whole action.

Seventh thesis describes the way how to recognize a breeding pair of wolves by tracks only in April before looking for wolf dens. Usually their trails are paired for the

most of tracked distance, and walking rate is noticeably slower than in other seasonal periods. The pregnant female prefers to walk slowly leaving wavy track trail like a dog (Photo 161). The pregnant female is heavy due to the final pregnancy. On soft substratum (sand or peat) an experienced wolf pup searcher may notice unusually deep footprints of such a female with wavy trail. One of the features of parent wolves is their busy that is evident for experienced gropers even from their track trails. For instance, father wolf never walks slowly on forest roads for more than several hundred meters, usually it runs. Parent wolves mainly do not walk faraway and do not mark much as non-breeders.

On the other hand, yearlings, which similarly to breeding wolves stay on a small area, walk slowly, location and trajectory of their track trails are characterized with not much sense, looks like that of loitering individuals. They carry and leave valueless things such rubber boots, plastic bottles and even human cloth. They collect and gnaw ungulate bones and antlers. This feature of rubbishing of yearling is rather noticeable and good to apply. All the above help a lot to distinguish tracks of wolf breeders from yearlings and other non-breeders.

(162–164↑←)*Ungulate bones that were gnawed by starving yearling wolves during their separate stay in late April–May, when they were sent away by breeding parents.*

(165)↑ *Wolf non-breeder with a toy.*
(166–168)↑→*Wolf yearling toys, when they stay alone in April-July.*

Eighth thesis, usually wolves locate their den not far away from the main road in the area that they have chosen for breeding. Parent wolves need to know what people do in their area by monitoring human-related situation from the den or being nearby. On the other hand, it is convenient for parent wolves to walk by the road, when they go for hunting and come back with food. Marking of borders of the denning area at the road seems to be also important for the parent wolves, and on such a road it can be done faster and more efficient in this very busy time. Moreover, just by such a road alien wolves may come into the denning area. So, such terrain roads are very essential for wolves at breeding. Nevertheless, that does not mean that wolves like breeding at a busy road. Such a road nearby the denning site may be quite small and rarely used by people, but anyway at the same time it is the main road that human uses to get the wild area. Really big roads with intensive traffic and their adjoining areas are normally avoided by wolves. For the majority of cases wolves choose not a busy terrain road (approximately up to 60 visits per day) by which people come into the area. So, do not avoid terrain roads in your searching for wolf pups and, while doing that, remember that pups may be situated not far away from the main terrain road. For instance, 2–3 km deep is already too much; if you appear in your searching more than 3 km away, it is very plausible that you are on the wrong way and need to come back. Also, see Chapter 4 for the details.

(169, 170) *In May yearling wolf is tearing jacket (below) and the jacket torn by the wolf (above).*

Ninth thesis, wolves prefer to situate den in places, where wild ungulates are not active a lot. These animals are real danger for small pups, and parent wolves know that very well.

However, despite the fact that wolves avoid places with many ungulates for denning, at the same time, places with rich prey (beavers and/or wild ungulates) supply needs to be located not far away (optimally it is 1–2 km). Also, see Chapters 4, 6 and 7 for the details.

Tenth thesis, presence of many brown bear or lynx tracks in a particular area usually (not always) means that this area is not a denning one of wolves, at least, at the moment. It is a worthwhile feature that provides time economizing for wolf pup searcher. Also, see Chapter 4 for the details, because in some situations a wolf den happens to be in a close proximity to a stay of brown bear or lynx.

Eleventh thesis is that killing by wolves of red foxes particularly vixen (mother red foxes) with cubs at their burrow-den is also a good indication that somewhere not far-away there are wolves at denning. Quite often you do not see any vixen that was killed by wolves at the burrow, you see only much digging of the burrow. Even such a digging looks like wolves would like to den there and enlarged the red fox earth. Nevertheless, actually they would like to kill the vixen and dug the burrow for her. In comparison with real wolf denning in red fox earth such a digging by wolves looks like more rough with more small digging tries.

Twelfth thesis is about the variety of wolf den types and which denning features can help and conversely which ones may confuse wolf pup searcher. From the beginning, we would like to state that wolves usually can create many dens in several denning areas (in our practice it was up to 79), whereas a particular single den exists from several hours to, perhaps, several days after the giving birth. It is because wolf parents replace pups from one den to newly created one all the time, especially, when there are too many mosquitos or the weather is rainy. So, if you find an empty recent den of wolves, it does not mean that the parents have replaced the pups far away before you arrived at this denning area. The pups may be very close, so, you need to continue looking for them in this denning area until the evening. As you may see on the various photos given after the Chapter 2, there are two basic types of wolf dens: an open couch and a burrow. Also, there is type of wolf dens like a burrow-den, but a burrow is not deep about 0.5-1 meter. Such a wolf den we call a cavity-den. In the case of an open den the smaller pups are, the deeper and narrower such a den is. Quite often breeding wolves create a burrow by enlarging badger sett or red fox earth (see on the various photos given after the Chapter 2), sometimes beaver burrow. Concerning types of wolf dens, it is important to know that all parent

wolves do open dens, but not all of them create burrows. Both members of breeding couple (*i.e.* the male and female) create dens. This feature is sometimes very useful to be taken into account, while you look for wolf pups. Digging activity of breeding wolves begins 5–21days before giving birth, whereas in the most of cases it happens about ten days before that. So, finding a wolf burrow does not mean that there are already pups nearby. Small open dens in kind of small pits state that either there are already pups or they will appear in few days maximum. However, such a pit with worn down look (for instance as on Photos 75, 80, 110 and 171) says about the presence of pups. Also, see Chapter 4 for the details.

The thirteenth thesis is mainly about possible distance between neighboring denning areas with different litters. Here it is worthwhile to notice that normally there are several denning areas for the same litter of a given wolf pack. It makes sense to consider this parameter, if the neighboring packs overlap in their home ranges. Otherwise, in the conditions of low population density in wolves, neighboring packs may be too remote for their consideration in the question. That means how far may be a den with another pups of another wolf breeders is to look for. In our practice in Belarus litters of such really neighboring packs were remote for 6–24, mean 16.7 km apart. So, the distance of 15–17 km is a good pointer to search for another den with pups, if the terrain is more or less densely populated by wolves. On the other hand, there may be two or even three litters in one pack within one breedeng group of wolves (*i.e.* the case of multibreeding in a pack). For instance, that happens when dominant male (the father) mated with daughters, too. In this situation of pack multibreeding the litters may be situated within smaller distance 0.4–4.2, mean about 1.2 km apart.

The fourteenth thesis is about wolf marking behavior during breeding period. Usually in pre-denning and denning periods breeders mark their currently occupied territory, but mostly not much. In this context

(171) *Open pit-dens of wolves in kind of a dimple to prevent creeping of the pups. Such a den is more typical for wolves during the first 10 days since mother wolf gave birth. If you find such a den with worn down look, that says about presence of pups.*

(172) *Wolf pathway coming to a den. In this case the distance to the den was about 600 meters.*

under marking we implicate the full procedure of marking with not only urinating, but also with scratching. Being at denning, the male breeder renews several marking points (1–7, mostly 2 or 3) that are mostly situated on the terrain roads not far away, but not nearby the denning area — usually about 1.2 to 2 km away. Also, see Chapter 4 for the details.

So, the given fourteen theses seems to provide the worthwhile knowledge about wolf denning that should be taken into account, while searching for wolf pups. Now, let us move on the procedure of wolf pup searching itself. It has several marked steps.

The first step is finding a small area, where a breeding couple of wolves stays before giving birth sometime in the mid-April. Normally in our own experience we begin at this step, and not when pups were born. While starting when pups were already born, it is easier to scare the parent wolves before you discover the pups. The features of presence of breeding wolves were

described before. After finding of the area, where breeding wolves stay, they should be regularly traced by their tracks on terrain roads only. Walking inside of the adjoining habitats is not recommended. The wolves may become scared. Conversely, wolves habituated to observe human activity on roads, and presence of people there less disturbs them. At the same time, even if you are very careful with the wolves, anyway, wolf breeders may change their stay a few days before giving birth. Approximately in one of four cases such a stay switch happens. If the breeding wolves have gone, we recommend to start looking for them again in 2–3 days, when their new stay has stabilized.

The second step is waiting for the time, when the founding male from the wolf breeding couple (or larger group) starts walking alone. It means that, perhaps, the breeding female has already given birth and stays with the pups. Actually, the heavily pregnant female may stay in a very small area of 3–10 ha up to several days (in our practice up to 4 days) before the giving of birth, and this feature may bring on further mistake. The mother wolf stays close to the newly born pups during the first 2–5 days (sometimes longer up to 10 days) and then it starts walking with the male at first not much, but then more and more. The time of one of the first together walks of the breeding pair could be the best chance to go inside the surrounding habitats in order to look for pups. Usually after 5–10 days stay in the denning area there are many wolf tracks, dens, claw marks on fallen trees, sometimes pathways *etc* and it all makes it easier to look for pups, when you discover the denning area.

However, the seemingly joining of the mother wolf (after the birth and initial stay with the pups) to the father wolf may be actually the last walking of the still pregnant female after few days rest in the chosen denning area. In this erroneous situation, if on this day you go inside of the surrounding habitats, you will scare the breeding wolves even before the birth still. So, to avoid such an undesirable event, if we are not sure that the breeding female has given birth, we continue waiting and monitoring

(173) *Latrine of mother wolf at den with pups. It consists of 11 scats, at least.*

(174, 175↑↓) *Resting site of a mother wolf nearby den with pups. After feeding pups wolf mother usually stays separately nearby the den, by avoiding to be suckled all the time escaping vellicating the nipples.*

the situation and do not go inside. If 2–4 days longer the couple goes for hunting more or less together, we begin looking for the wolf pups there.

Nevertheless, the above delay may be a problem, too. Breeding wolves, being worrying the entire time, tend to change the denning area. Respectively, the scenario may be the following. You waited some extra time (2–4 days as it was recommended), while actually the pups have already been born (*i.e.* the absence of the breeding female during the first few days

(176-179↑↓) *Uncompleted and not used pit-dens of breeding wolves. Searching for wolf pups, you may face with denning habitats without relevant substratum to see enough wolf tracks. In such complicated places, you may get very useful feature of the den presence nearby. That is unfinished and usually not used pit-dens like a some digging mostly in a sheltered places.*

(180, 181↑↓) *Much urinating of breeding female wolf in the denning area. When the mother wolf stays most of the time with newly born pups, sometimes, it urgently needs running away for urinating and defecating. Mother wolf does these 0.2–1 km, usually 0.3–0.5 km away from the den with pups. In particular, if you found much urinating by female, it mostly means that the pups are not far away, because of normally wolves urinate a bit economizing urine for the further marking. In the case of mother wolf, it tired to avoid urinating at the den, but when it appeared away spending easily all the urine accumulated.*

actually was because of giving birth); the breeding wolves found much human activity on the road (you use the roads for their checking); and finally, they have gone with the pups. You go inside of the denning area in the habitats nearby the road and find empty dens. Such a scenario may happen easily.

So, we never know what can happen with wolves at breeding. Sometimes, the better seemingly reasonable decision becomes the worst one. There is no an entirely reliable recommendation, when to go inside the presumably denning area at the road you inspected, taking into account splitting and joining of the breeding female and its male.

However, we need to come back again to the second step, *i.e.* our actions during the track survey of breeding wolves on roads around their denning area. It is not only registration of the described splitting and joining of the breeding female and its male. Another main thing is to learn the directions of the founding male's way. The father male goes hunting from the den in different directions, his trails are usually not so straight, and almost there is not much running, mainly trotting in its moving patterns. Conversely, coming back to the den, perhaps carrying food, the father male uses running quite a lot, goes straight to the den, and the last 1–2 km of the way it goes by the same route even sometimes creating like a pathway. Actually, it is not a well tram-

pled one, but it is 5–20 m wide moving stripe. Moreover, when the father wolf appears on the nearest road, while going hunting, it tends to walk by the road fairly far (perhaps, searching for prey during this walking). In contrast, coming back with food, the father wolf frequently just crosses this road. It may be a worthwhile feature to recognize which kinds of its trail you faced. In finding of den-directed passage of parent wolves morning dew and recently grown wood cover can help you, of course, but anyway the main place to see their tracks are still terrain roads. Also, presence of people on roads is more habitual for wolves, but whereas checking track on dew or grass aside of roads, it is easier to scare the breeding wolves. So, the groper should find and recognize such passages of the father wolf by which it straightly reaches the den. Usually there are several passages like this. Crossing of them on the map, you indicate the location of the denning area, sometimes, surprisingly precisely.

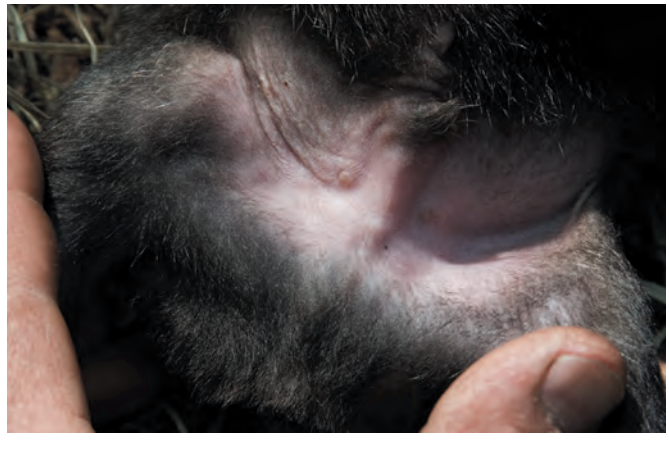
The third step needs to be undertaken, when you are sure that you found the father wolf passages, which lead to the den, and if you believe that the pups are still somewhere there, where the passages lead to. If it is so, you need to begin detailed inspections of the area, where, perhaps, there is the wolf litter. Such a search should be started early in the morning, because you may appear to be very pressed for time in discovering the pups. First, it is not easy to discover the denning area and, second, it takes much time to find all the dens produced by the parent wolves. For instance, there may be two opposite situations: you may discover the pups in the third den found and then you will find fifty more previous dens around or, conversely, you may discover the pups in the fiftieth den found and then find only three more other dens around. Finding yourself in the second situation, you will spend five more hours, at least. Searching for the denning area, you need to follow the directions of passages, by which the breeding wolves regularly returned to the den, or just follow one of these passages. On the way you

(182) *Wolf pups in denning site.*

need to inspect the relevant habitats that were highlighted before as most suitable ones for breeding in wolves (see the second thesis). Nearby the denning area you may face well trampled pathway of the parent wolves. This pathway goes to one of the dens, *i.e.* active one or previous one left several hours or days before. There are more or less marked paths between the consecutive dens. Following these paths and doing detailed inspections of relevant places, finally you may find the pups. We strongly suggest to follow the between-den paths, when you find a very recent den without pups. Try to find the next one by tracking parent passage, which was created, when they replaced the pups. Usually, it is more or less not too complicated to find the active den in the denning area found, if there are relevant habitat types. For instance, such habitats may be either thickets with many uprooted trees (if it is not too large tree fall) or thickets in logging areas with wet soil and recently grown grass or abandoned peatory with peat walls left-off. Conversely, you may face logging area on dry land or above-mentioned sand-dune habitats or any other mostly dry land forest without relevant substratum to see enough tracks.

In such complicated habitat types of wolf denning area, you need to do the area-wide inspection. Doing that you may get very useful features of the den presence nearby. First of all, that is unfinished and usually not used pit-dens like some digging, mostly in a sheltered places. It should be maximum of such preparations several hundreds meters around the active den. Another feature that helps to find wolf den is female' urinating and defecating presumably already in the denning area somewhere on the way. When the mother wolf stays most of the time with newly born pups, sometimes, it urgently needs running away for urinating and defecating. Mother wolf does these 0.2–1 km,

(183, 184↑↓) *Genitors of a female pup (above) and male pup (below).*



usually 0.3–0.5 km away from the den with pups. Quite often it is rarely used terrain road or some dry land opening. In the mother's latrine site, usually there are 2–6 scats placed 1–15 m apart. In particular, if you found much urinating by female, it mostly means that the pups are not far away, because normally wolves urinate a bit economizing urine for the further marking. In the case of mother wolf, it tried to avoid urinating at the den, but when it appeared somewhere away it spends easily all the urine accumulated. Twice we found wolf pups with this feature being in seemingly unpromising situation with denning area within dry land habitats.

The action may be finished on the third step described above. Nevertheless, the denning area may be missed by the groper, and then the daytime may be spent by trying to find the denning area farther from the starting point. Also, another bad luck may happen, *e.g.* the groper may spend almost all daytime within the large and complicated denning area, by gradual discovering new and new former dens. Then the groper has no time to discover all of them and one with pups. With sunset it appears impossible to continue the work and this implicates that the wolf pup searcher has failed today. During the comming night the parent wolves will take the pups away from the disturbed denning place and several next days the parent wolves will gradually replace the pups with each replacement for 1–4 km away. Shorter and longer replacements of litter than 1–4 km away are registered less often. However, during several days of pup replacement they appear on the distance of 3–8 km (in our own experience up to 12 km, more often 4–5 km) from the previous denning area. In this case, when you have scared the parent wolves and they replaced the litter, the whole procedure should be started again. Here it should be noticed that further searching for the pups of scared parent wolves is usually a very hard job. Scared breeders tend moving with pups changing den spots unusually often.

Quite often wolf pup searcher faces the habitats, where it is too complicated to discover den with pups. For instance, it may be too homogeneous habitats with rather equal their sheltering and without sufficient abundance of terrain roads. In this case it may be even useful to scare the wolf family from such habitats in order to get them somewhere else in the neighboring area, where it seems to be easier to find wolf den.

Anyway, after scaring of wolf family with small pups, first, you need to wait for two days, better 3–4 days and then try to find their new denning area traveling a lot by terrain roads. However, you need to take

into account that the disturbed parent wolves became even more careful and they may be easily scared again. Moreover, such disturbed parent wolves replace pups without evident disturbance nearly every day. The distance between neighboring dens, which they do in this situation, is usually 30–200 m, but sometimes up to 0.8 km.

Since 2014 we also applied camera-trapping (up to 70 camera-traps) for gaining additional useful information about breeding wolves such as registration of heavily pregnant females, females in lactating, their pups etc. However, we have always avoided to install camera-traps at an active wolf den.

To investigate denning behavior in wolves, simultaneously with wolf pup searching in May and afterwards in June we looked for all denning sites of a given breeders and described them. Some den sites have many dens (a range from 5 to fifty, to 79 in one of them). Displacement distances were calculated between the center of the natal den site to the center of secondary den sites as the straight line distance between them, and were measured using a GPS. We also examined whether the number of burrows differed from the number of surface dens between the den sites. When we found pups in a den, they were handled, counted and their sex was determined.

In autumn, we assessed the number and distribution of surviving pups in a given litter by howling at night to locate them within the pack home range (usually they answer easily). While howling in day-time nearby the place, where pups stay, sometimes the pups run to us and we saw them and, so, could count them, too. A total there were six such cases of visual counting pups in early autumn. After that, we inspected the discovered housing area of pups stay, and that scared the parents. They usually relocated the pups, travelling on or crossing one of the numerous roads mostly with sand cover. On such a road we could count pups often fairly precisely. In 2014-2019 camera-traps helped to assess how many pups from a particular litter survived till autumn. All these data helped to determine the litter size in early autumn and the pup survivalship. Later in November, we could count the number of surviving pups because of their smaller footprints in the first snow. Also, camera-trapping is very helpful for that question.

At the same time, we estimated indices of mosquitos abundance, rainfall and disturbance of the breeders by human (*e.g.* logging in the area and other human activity). Environmental conditions were assessed from spring to mid-summer using a Likert-type scale with a few categories (1–4 or 5) (Likert, 1932). Mosquitoes abundance was

evaluated from our own assessments (no insects; low, medium, high and very high abundance) several times during spring and mid-summer; rainfall from our own assessments and some registrations from the state weather reports of the adminisrative district of the study area (150–200 mm per month: drought; 200–300 mm: medium, normal year; 300–360 mm: rainy weather). Human disturbance was evaluated simply by counting from a light human presence (like a vehicle passed) to heavy human activity like logging or tourism (*e.g.* 10–20 people with motorbikes, or camping during a few days; increasing density of roads and houses near the denning area). From these two extreme situations, we defined four categories: no disturbance, low, medium, and high disturbance.

A total by such a way over 15 years, we documented in detail 30 denning areas and pup survival there. These data set was analyzed statistically.

Here we would like to say more detailed about the sample size of the wolf litters that we inspected, because in the different items of this book it is so different. The reasons are as following. First, because the reproduction parameters, which we could assess, were highly variable. For example, in one case we found wolf denning site with many dens and pups that were present there, but we did not count pups precisely

(185 186↑↓) *Game bags of wolf pup searchers. That was one of the data source to estimate wolf litter size.*

because they were already quite big and escaped from the den, while we were approaching them. So, from that case we could only record information about denning habitat, number of dens in the denning site, and approximate age of the pups (we saw a pup that was running from us). In another case, we could discover a wolf den with pups of early days, count and sex them, then we traced the most of further denning details and estimated the number of pups that survived till winter. Between these two polar situations it may be many other intermediate situations, which reproduction parameters were registered in a given case in connection with our possibilities and opportunities that were related to the breeder behavior. Another thing is that for some questions (for which it was obviously correct) a part of the data were taken from other wolf-related people *e.g.* wolf pup searchers. We merely use not our own data in the cases, when they were gained from wolf-related people, whom we know the life-long and trust them (mostly three wolf pup searchers, Aliaksandr Hurin, Victar Staliarow and Lianard Yurevich). Anyway, in many places of the book we used that just we found 75 dens with pups what was with different amount of information obtained in those cases.

3.5. Estimation of wolf fertility parameters

So, searching for wolf pups, we are able to assess the size of wolf litter with pups of early days. This litter size is more or less the same as fecundity that was estimated as number of developed embryos per pregnant female wolf in the mid-April. Wolf litter size was assessed not only from own data that were collected through searching for wolf pups, but also from the game bags of other wolf pup searchers. Also, we investigated reproductive organs of many female wolves, which were killed in March-April, to assess the wolf fecundity and female's taking part in reproduction.

To investigate wolf carcasses was non-limited in our study areas and Belarus, because each year in the country usually there were killed from 600 to 1200 wolves; maximally - about 1700 wolves in the cold season 2016-2017. We guess that these values were markedly overestimated by the rough hunting statistics in Belarus; perhaps, in the reality the wolf number, which were annually killed, was 10% to 50% less, but anyway such a material for the study on wolf carcasses was not a hard available. Approximately 90% or even more of wolves, which were killed by hunters during a year, actually were hunted in the period of the mid-October till the mid-April: 50-60% till the end of February and 30-

40% in March-April. So, we had the perfect possibility to trace the frequency of wolf female's breeding and the species fecundity. That was more the matter of vacant time and other recourses to investigate that. Also, we were more limited with usage of such data for analysis, because of for that we needed, at least, sufficiently veracious data on the wolf population density and prey supply. Therefore, we failed to gain very detailed view on the wolf fertility in Belarus, however, a lot of interesting fertility estimates were obtained anyway.

3.6. Investigation of wolf pack composition

We defined wolf pack composition by several parameters and characters. When we deal with a wolf pack, the maximum information that we would like to gain about its composition are: (1) number of individuals, (2) number of pups of the year, *i.e.* the current biological year, 0+, (3) are there two dominant individuals, *i.e.* breeders, breeding adult male and female or is there only one dominant strong wolf? (4) respectively to the previous characteristic whether it is mainly family-originated pack or pack that consists of subordinated individuals that were gathered by the strong dominant wolf or may be a newly appeared pair of strong wolves? (5) number of subadults 1+ (pups of the previous biological year) and other subordinated individuals. Of course, that was a maximum information we would like to learn about a wolf pack, but in the reality we usually get know less.

Such information was collected by us through wolf census, with help of marked wolves (pup finger clipping), camera-trapping and particularly while investigating wolf carcasses of the packs that were entirely extirpated by hunters.

As it was mentioned in the previous item, such material was non-limited in our study areas and Belarus due to intensive game harvesting of wolves each cold season. So, during about 30 years of interest to wolves and nearly of 20 years of intensive study on the species we investigated a lot of wolf carcasses, but with very different details: from checking is it 0+ or elder wolf and looking at female's reproductive organs to the whole variety of studies on a carcass with exact determination of age *etc.* The sample sizes we gained are given in the result items.

(187-190↑↓) *Game bags of wolf hunters with a fladry.*

3.7. Study on the interference between wolves and lynxes

In 1997-2017, to check interference between wolves and lynxes, we applied a lot of snowtracking of both species (a total about 2,300 km of wolves and 1,400 km of lynxes), camera-trapping with up to 72 cameras (in 2014-2019 only) and a lot of habitat inspections, during which such useful was gathered, too.

3.8. Gathering of scats of wolf pups and their parents, analysis of the scats in order to estimate the pup and parent diets

Scats of parent wolves were collected as relatively big wolf scats in the denning sites. Generally, there was no any hassle to collect enough scats of parents. It was not so easy to gather scats of pups, even when we knew the place of their stay. In June and

(190↓) *Fladry to hunt on wolves.*

quite often till the mid-July the majority, (sometimes all) scats of pups are collected by their mother, perhaps, by both parents. Parents carry the pup scats in their stomachs (like in a bag) away, where they drop all of them by vomiting. So, we could gather pup scats in the period of late July till the end of September.

Studies on the diets of pups and their parents were carried out with scat analysis. The scats were washed and undigested remains were dried according to a technical process described in Jedrzejewska and Jedrzejewski (1998). Mammal hairs were identified microscopically using the keys of Debrot et al. (1982) and Teerink (1991). The frequency of food type occurrences was calculated by the ratio of the number of scats containing a certain food item to the total number of scats analysed. Percentage of consumed biomass was evaluated from the dry weight of undigested food remains using coefficientsof digestibility, *i.e.* the ratio of the fresh weight of a given food item to the dry weight of its remains in scats (Jedrzejewska and Jedrzejewski, 1998).

(191) *Vadim Sidorovich is checking camera-trap.*

3.9. Determination of wolf age

While investigating composition of wolf packs, which were eliminated by hunters, age of wolves was determined by the method based on tooth (mainly canine) cementum banding according to Klevezal (1996). This cementum banding was investigated on coloured transversal or longitudinal slices of decalcified canine roots (Klevezal, 1996). Only clearly seen and entirely formed incremental layers were counted.

Also, quite often we needed to get know, it is pup of the year, *i.e.* 0+ or older individual, what was investigated by looking in the canine pulp; in young wolf 0+ it is evidently broader than in older wolves because of continuous deposition of dentin.

The information on tooth wear and occlusion of canine canal were additionally used for wolf age determination (Gibson *et al.*, 2000).

(192) *Wolf pup scats that were collected in early September.*

(193) *Wolf parent scat.*

3.10. Estimation of the population density of the main prey species

Beavers were censused by counting of their settlements in the period from November to April following the method proposed by Kudriashov (1973). Active beaver den in kind of either burrow or lodge having a winter food store nearby (or its evident remnants) was assumed as evidence of one beaver settlement. In the past, when furbearing was popular, and beavers were trapped regularly, from one to 12 individuals, on average about four beavers were recorded in one their settlement (Djakov, 1975; Dezhkin *et al.*, 1986; Balodis, 1990). However, we would like to notice that nowadays, trapping of beavers declined in Belarus and numbers of yearly trapped beavers is not high. Perhaps, in this situation more beavers live per one settlement on average. For instance in Naliboki Forest, where beavers were sporadically hunted, indeed higher mean number of beavers seems to compose one settlement. In 13 beaver settlements investigated in 2002-2006, from 2 to 8, on average 5.4 beavers were registered. By establishing census of beavers, we applied two approaches: first, beavers were censused along model watercourses of various types, second, we did total census of beaver settlements on particular plot of 15-30 km^2. Such terrain fragments were chosen in those parts of the

study area, in which habitat structure seemed to be rather typical.

In Naliboki Forest wild ungulates were censused on the same plots of 15-30 km^2 as beavers. Visual counting of wild ungulates was undertaken by wavy inspection of the census plot by effort of 2-4 workers from plot centre to its periphery. If a wild ungulate individual or group (*e.g.* wild boar Sus scrofa group) was scared without sufficient visual observation, we tried to find out the number of individuals by inspecting of the trail. Such inspections of the census plots were done 2-3 and more times per winter. Finally, we assumed approximate number of individuals of each species that inhabited the plots during winter. The data gained in such model plots were extrapolated for the whole study area. Population biomass of wild ungulates and beaver was calculated by multiplying of the species density estimated and average body weight taken from the literature (Kozlo, 1983; Jędrzejewska & Jędrzejewski, 1998).

In Paazierre Forest and some other areas we used estimates of population densities of wild ungulates and beavers, which were produced by wardens of game husbandries or nature guards of protected areas. In these cases usually we checked roughly the veracity of such an information.

3.11. Statistical methods

Simple descriptive statistics, Spearman's coefficient of rank correlation ($r_{s)}$, Mann-Whitney's U-test, Student's t-test for difference between two means, G-test for examining heterogeneity of percentages were applied for statistical analysis of the data obtained in accordance with the standard recommendations (Sokal & Rohlf, 1995).

Chapter 4. Breeding behavior in wolves

In this chapter we present our knowledge on the breeding behavior of wolves in Belarus, mostly in Naliboki Forest and Paazierre Forest. Describing the species breeding behavior, we distinguish three main breeding stages: mating; denning and tending of early days pups; and raising of pups older than 50 days. In this book under breeding behavior of wolves we define the aspects of the species sociality, movement, pathways, marking, creating dens and usage of habitats *etc.* during the main breeding stages as well as seasonal timing of the breeding stages.

All knowledge was gained by tracking of wolves, investigating of wolf carcasses, by means of camera-trapping, inspecting relevant habitats *etc.*, whereas our visual observations of wolves were poor due to shy and ambush behavior of wolves. So, such behavioral acts as a courtship before copulation and other similar behavior were out of our study possibilities.

Denning behavior of wolves was the most interesting phase for us to study on, because this phase is crucial for the reproduction success. As to our opinion, this phase is not yet sufficiently investigated in Belarus and the whole Eurasia, before our study appeared. However, there is a lot of knowledge about wolf breeding behavior and denning in North America, but those patterns are very different from the ones in Europe (Mech & Boitani, 2003 and references therein; Sidorovich *et al.*, 2017), perhaps, because of the long-term and separate evolving of the wolves in distinctive environments, with too many differences in the ambient conditions.

Concerning the publications about wolf denning behavior in the European forest zone, mainly studies conducted in the Polish part of Bielaviezha (Białowieża) Forest, (Theuerkauf *et al.*, 2003; Schmidt *et al.*, 2008) were based on telemetry methodology with a few breeding females that were followed (n=6) and a rather a small number of dens that were investigated (n=8 and 16, respectively). To us, it looks like the searching for dens and checking of denning sites in the mentioned studies were scrappy: Usually there are 10 to 30 used dens in only one wolf denning site according to our study in similar habitats of densely forested terrain, such as in the reserve of Naliboki Forest (Sidorovich *et al.*, 2017), which is only about 140 km eastwards from Bielaviezha Forest. Quite often an initial wolf den as well as others exist less than a day, and the number of dens increases quite fast in a denning site. The few dens that were inspected in the Polish part of Bielaviezha Forest, are evidently not

enough to understand and to make statements about the wolf denning behavior in the diversity of behavioural features in the variety of denning habitats. There are also other shortcomings of those results, for instance, related to the mutual distribution of breeding wolves and yearlings. Perhaps, all these disadvantages connected with greatly insufficient efforts that were invested in the checking of denning sites, being busy with telemetry itself. Also, the too small sample size biased the results. The results on the wolf denning behavior in the European part of Russia (Danilov *et al.*, 1985) are too short and descriptive. Actually, the authors (Danilov *et al.*, 1985) did not fix the denning behavior as the main aim of their study on the wolf reproduction; they were targeted on the demography effect from breeding and on fertility of wolves. Therefore, despite of the existence of the above-mentioned publications, we state that actually there is not a lot of correct knowledge available about denning in wolves in the European forest zone.

4.1. Mating in wolves

According to our collected, diverse information (carcasses that were checked, trampled copulation spots on snow cover, female's urine containing a bit of blood that indicates a proestrus phase), it is clear that the majority of adult wolf females mate in the first two decades of February (67%, n=216). With the exception of one registered case, the earliest copulation of wolves was registered in the first decade of January, whereas in March we still registered estrus in a few females.

The mentioned exception was as follows. On the 26th of November 2016 in Naliboki Forest we photographed a female wolf, which was seemingly pregnant (see Photo 194). We had no doubt anymore, when not faraway from the camera spot in the late February 2017 we discovered the winter wolf denning site with 17 dens. The denning site was used more than month ago for a quite long period:20-30 days. That place is situated 2.1 km from the spot, where the photo of the pregnant female was taken. In May 2017 we observed 4 surprisingly big wolf pups (5-6 months old) in the place that is situated on a distance of 3.9 km from the camera-trap spot, where the photo of the pregnant female was taken in November. Thus, having all these findings, there was no doubt that the female wolf got pregnant in late September. The possible cause of that breeding peculiarity could be connected with the female's loss of litter in May 2016. Just in the place, where we observed the unusually big pups in May 2017, in May 2016 there were poached wolf pups. So, it was in the core area, where in November 2016 that pregnant female wolf was registered.

One of the important behavioral questions of mating in wolves is in which social group of wolves mating behavior and copulation itself happens. For instance, Schmidt *et al.* (2008), basing on quite limited material (only 6 radiotracked females), concluded that the mating pair did not separate from the other pack members for mating. On the other hand, the large, but more scattered materials on wolf mating from Russia suggests quite the opposite (Danilov *et al.*, 1985). Danilov *et al.* (1985) also told about a large mating group of wolves having no offspring and consisting of adults only, presumably non-relative ones. We will say that in Belarus both situations in mating of wolves are present, perhaps, with not much prevalence of any one.

In Belarus during mating season for wolves, we commonly found that a mating pair walked for a long time without any contact with other wolves. In two cases we registered two breeding females and one male. Such an option of a mating group in wolves (*i.e.* one or two breeding females and one adult male) constitutes approximately a third part of the respective information on the question. In the other registered cases, there were more wolves included in a mating group. However, by using snowtracking only, it was hard to say which other wolves followed the mating pairs. However, the information that we gained from hunters, when the whole group of wolves was killed (by using hunt-drive with fladry or shooting wolves from a helicopter), may suggest more. We learnt that about another third part of wolf groups with a mating female was indeed a normal pack with pups of the year or (and) yearling wolves (1+), presumably the pups of the previous year. Also, in such a family-originated pack it may be present one or two other adults (females or males) in the mating period. These extra adults were mainly females in estrus, too. So, in such a wolf family group there may be one to three breeding females during the mating period. When wolf persecution rate increased, the frequency of such a family-originated mating group declined. Hunters kill pups easier, so consequently families disappeared. We registered the same trend, when lynxes got common in the Naliboki Forest; lynxes kill most of the wolf pups (see Chapter 6), and family-originated packs of wolves simply almost disappeared.

Another third part of the hunter-related material on mating sociality in wolves suggest that during mating season in the wolf population there are many mating groups that consists of one or several breeding females and two or more (up to seven) adult males. Once in Paazierre Forest, a mating group of wolves was killed, which consisted of one breeding female and 8 big males. In such a case only one male follows

the female in estrus very closely (walking just behind it), whereas other males, *i.e.* the mating competitors follow the female few hundred meters behind. It is the same as it was reported by Danilov *et al.* (1985) in Russia, but was not registered somehow in Poland (Schmidt *et al.,* 2008). The only too small sample size in the Polish study may explain that.

Also, we would like to add that among the 27 checked wolf groups that were entirely killed in February (*i.e.* mating period for wolves) there were revealed 6 groups consisting only of 3-6 non-breeding young individuals in the first or second year of life.

Thus, all the above material suggests that in Belarus quite often a wolf mating pair separates from the other pack members for mating. We also assume that in a large protected area with no elimination of wolves, there is considerably higher portion of non-separated wolf packs during mating season. On the other hand, the higher the

(194) *The registered pregnant female wolf on 26th November 2016 in Naliboki Forest.*

rate of wolf persecution by human, the more frequently the above-described mating groups of many adults only may be registered. Across wolf elimination actions, a portion of lone adults and small groups (2-3) of adults increases considerably, because of more experienced adults save themselves easier than young wolves. In turn, this situation with lone adult wolves leads to the emergence of mating groups consisting of adults only in mating season. Maybe therefore Schmidt et al. (2008) did not found such a pattern of mating groups on their rather small gathered material set in the Polish part of Bielaviezha Forest, (cf. only 6 females were followed).

We have got anecdotal information on how far the breeding wolves and the other members of the pack stay from each other during mating in the case of a temporal separation of the pack. By means of snow-tracking and with help of marking of pups with finger clipping, we estimated this distance sufficiently precise in seven situations. First, it should be stated that this distance is a greatly changeable parameter, because of both the mating wolves and the other pack members move all the time. Breeders were more mobile and walked for about 19 to 36 km per twenty-four hours, while the remaining subordinated parts of the packs, mostly consisting of young wolves, moved markedly less and sometimes stayed in a relatively small area (2-5 km²) for several days. Anyway, the distance between the mating breeders and the other members of the packs was estimated as 2 to 13 km, mean 4.9 km.

Thus, in Belarus, mating in wolves mostly happens within the following three social situations: (1) a mating pair only; (2) a whole pack of family origin which includes pups of the current and (or) previous biological years, with one to three females in estrus, sometimes, additionally may be one or two other adults; (3) an adult group with one to three females in estrus and one dominant male that tries to keep the breeding females for himself, whereas others males (usually one to four) keep a security distance, but tenaciously follow the mating group. If the rate of wolf persecution by humans is low or moderate, these three mating situations are more or less equally present in both protected areas and game areas. With increasing of rate of wolf persecution by hunters, or when lynxes reach moderate to high population densities, the second social situation, in which wolves reproduce (a whole pack of family origin) becomes rarer.

4.2. Wolf denning and tending of early days pups

In the method chapter, we already presented a part of our knowledge about wolf denning in Belarus as far as it was necessary to provide sufficient knowledge background for explaining the methods how to search for a wolf den. In this item, we will give our gained findings on the wolf denning behavior more thoroughly, but anyway you will find several duplications in the texts. It should be noticed that with our approach to study on the wolf denning (without radiotracking) we were limited to estimate precisely the wolf movement in this period. Nevertheless, being concentrated on the wolf denning itself, we succeeded to learn other denning characters in a very detailed way.

Despite of the fact that we could not measure the precise movement of breeding wolves in the pre-denning period, nevertheless, even with track information it was very noticeable, when breeders have switched their behavior for denning. It means they start to stay in a rather small area, only having pronounced homesites, where the breeders stay most of the time.

Here it is important to define that under the wolf breeders at the denning stage we mean one or several pregnant females with an adult male or sometimes several males. Additionally, it may be a non-pregnant female amongst the mentioned breeders. Mech & Boitani (2003) called such an extra individual at denning an 'adoptee'. However, as the adoptees role and origin is still ambiguous and disputable, we avoid this term. We definitely know that besides of the breeding pair (*i.e.* a pregnant female and its male (perhaps, the father of the coming pups) there may be other allowable individuals, both relative or non-relative ones. We are certain that they help with foraging and protecting pups at the den. Hence, when we say 'wolf breeders at the denning stage', it means either a breeding pair or such a larger breeding group. Usually the breeders send the rest of the pack members (mostly yearlings) away.

An interesting question to answer now is how far from the breeders this 'non-breeder part' of the pack stays. To our findings, it is quite rare that they stay in the proximity from the actual denning site, nevertheless, both situations were revealed in our experience. According to our information that is based on tracking, marking of pups and camera-trapping, usually this distance between breeders at denning and yearlings varied between 3 and 8 km.

The above-mentioned behavioral switch of breeding wolves for denning happens usually about 10-15 days before parturition. The breeders start to stay on this rather small area up to 20 km^2, usually 8-12 km^2 only. In this pre-denning period the pregnant females stay a lot in the denning site

Table 4.1. Initial data (full data set only) on the wolf denning behaviour in relation to some factors, Paazierre Forest and Naliboki Forest, Belarus

Number of pups in May (in September)	Number of dens in the first site	Number of dens in the second site	Number of dens in the third site	Number of dens in the fourth site	Distance between the denning sites in km	Mosquitos, from 1 to 5	Rainfall, from 1 to 5	Human presence, from 1 to 5
7 (2)	26cd, 5b	47cd, 2b	33cd	-	3.2, 4.1	3	4	4
9 (2)	51cd, 1b	14cd, 5b	6cd	62cd, 2b	1.7, 2,9, 5.6	4	5	4
4 (3)	20cd, 4b	3cd, 3b	6cg, 1b	13cd, 4b	1.3, 3.0, 4.7	3	2	2
6 (5)	27cg, 3b	32cd, 1b	10cd	-	2.2, 2.9	4	2	1
3 (3)	72cd, 5b	5cg, 5b	4cd	22cd	3.0, 1.9, 2.0	3	1	4
5 (3)	9cd, 2b	19cd	-	-	4.2	3	3	2
8 (4)	62cd	-	-	-	-	5	2	1
7 (6)	20cd, 3b	4cd, 4b	3b	17cd	2.3, 3.0, 1.1	2	1	3
4 (4)	14cd, 3b	12cd, 16b	10cd, 4b	-	1.3, 1.9	4	2	2
5 (1)	32cd	79cd	14cd	-	3.4, 4.9	5	5	3
7 (4)	21cd, 4d	19cd	-	-	6.0	3	2	2
6 (6)	11cd, 1b	17cd	6cd, 5b	29cd	1.7, 2.0, 2.2	1	2	3
5 (3)	29cd, 4b	-	-	-	-	2	2	2
9 (2)	44cd, 4b	21cd, 5b	26cd	12cd, 2b	3.9, 1.1, 6.7	4	4	2
6 (2)	27cd, 2b	-	-	-	-	3	2	2
6 (5)	44cd, 3b	-	-	-	-	2	4	1
9 (6)	5cd	24cd, 3b	11cd. 1b	7cd	2.6, 3.0, 1.1	3	1	3
4 (4)	6cd, 7b	5cd, 4b	-	-	3.0	1	1	2
2 (2)	22cd	11cd	6cd	-	2.5, 1.4	2	2	2
6 (4)	19cd, 2b	7cd	8cd	13cd, 1b	2.9, 3.6, 1.8	1	3	3
7 (3)	4cd	39cd	8cd, 4b	-	4.8, 5.2	2	5	3
10 (3)	15cd	3cd, 4b	38cd	-	4.2, 3.9	2	5	3
1 (1)	7cd	22cd, 2b	-	-	2.4	4	3	1
5 (0)	26cd	15cd, 2b	13cd	-	4.0, 2.9	4	4	3
8 (0)	42cd	9cd	10cd	-	6.5, 3.9	5	3	2
3 (0)	29cd, 2b	47cd	48cd	33cd	3.9, 4.4, 3.8	3	5	4
6 (2)	11cd, 3b	10cd	6cd, 3b	31cd, 4b	6.1, 4.5, 6.2	4	4	4
7 (1)	9cd	14cd	9cd	16cd	4.4, 5.3, 7.0	5	4	3
7 (5)	5cd, 6b	15cd, 2b	4cd, 2b	10cd	1.8, 2.0, 1.9	2	2	3
8 (3)	42cd	-	-	-	-	2	2	2

chosen, walking less and less with shorter and shorter radius of 0.6-2.2 km. Around this time *i.e.* 10-15 days before parturition, breeders begin to dig a lot. This results in many small pits, deepened couches, enlarged entrances of badger setts or red fox earths, self-made burrows or just some attempts to create a burrow like an entrance only etc. in the denning site.

It is easy to recognize the tracks of the breeding wolves. The pregnant female prefers to walk slowly, leaving a wavy track trail, like a dog trail. For her even walking is heavy, due to the pregnancy. On soft substratum (sand or peat) a heavily pregnant female leaves unusually deep footprints. The track trails of male breeders suggest that they are very busy. In this pre-denning period as well as during denning, male breeders never walk slowly on forest roads for more than several hundred meters; usually they run, sometimes trotting.

On the other hand, during the wolf denning period also yearling wolves stay on a small area (up to about 70 km^2, usually 10-20 km^2 only). Left alone, they got shy and walk slowly, location and trajectory of their track trails are characterized with a random pattern not making much sense. Their track looks like that of loitering individuals, in addition they carry and leave useless things such as rubber boots and plastic bottles on their way, and they collect and gnaw on ungulate bones and antlers. All the above helps a lot to distinguish tracks of a breeding wolf pair from a yearlings trail and that of other non-breeders.

Here it should be pointed out that parent wolves may carry such 'stupid things' too, while bringing them for their pups to play. Such a toy is bitten by small thin canines of small pups and lie around dens, while toys of yearlings are forgotten a lot, at roads usually. In Belarus at two-thirds of the inspected wolf denning sites we found pup toys. About a half of them were small things of man-made origin, others were mammalian bones and antlers.

Concerning wolf breeder marking behavior in pre-denning and denning periods; they mark their currently occupied territory, but mostly not a lot. In this context, marking covers both urinating and scratching. Being at denning, the male breeder renews several marking points (1–7, mostly two or three) that are mainly situated on the terrain roads not far away, but not nearby the denning area — usually 1.2 to 2 km away. Only rarely we saw the parent wolf scratching close to the active denning area. So in general, there is a low rate of marking and a 'hidden wolf life' in the area of 1–2 km around the den, lasting at least a month after parturition. The exception is the female's scats and its urinating, which is done within the denning area because all the time it has to guard and take care of pups of few days old. As to yearlings that

stay alone, they do not mark or only rarely do some marking. In the wolf breeding period the packs without a litter tend to continue marking intensively and mark their own territory, *i.e.* the home range widely (much bigger area than a denning area).

Also, it is worthwhile to notice that 2–5 days before the parturition, it looks like the marking behavior of the breeding wolves suddenly nearly stops. While actually, the parent wolves continue some marking in a few spots.

(195, 196↑↓) *Toys of wolf pups.*

In Naliboki Forest and Paazierre Forest in Belarus, wolves usually use the following denning habitats: thickets with many uprooted trees, especially spruces; thickets in logging areas with a lot of tree remnants and timber left-off; abandoned peatory with peat mounds left-off; and small sand-dunes with young pines and small openings at the border with boggy habitats having dense ledum and bilberry shrubs. When there are too many wolf-inimical animals such as lynx or wild ungulates, wolves shift their denning in coniferous stands almost without underforest and poor forest floor where both lynxes and wild ungulates are not so common (see Chapter 7 for details).

In Naliboki Forest there are large meadows on drained lands surrounded by dense forest habitats. Such a meadow may be used by wolves as a denning habitat, when the height of the grass stand is about 40 cm and taller. Within grassy openings pups may be placed either nearby the opening center or at its edge at the border with the forest. Closely located terrain roads are not avoided by such families, if the grass thicket is sheltered enough. In grassy openings wolf parents evidently prefer to place pups at drainage canals, if they are present there. Sometimes, there wolf parents dig burrows preferably in canal banks or on relatively

higher plots with a sand layer. The evident benefit of such a denning habitat is as follows: rather low abundance of mosquitoes, easy watching of surroundings, well-sheltered environments for pups and quite often for parents as well. During too rainy weather, pups may be temporarily replaced to the neighboring forest or they stay in burrows. If nobody disturbs the wolf family, they may stay in such large meadows until mid-October.

Usually wolves locate their den not far away from the main road in the area that they have chosen for breeding. Parent wolves need to know what people do in the area by monitoring human-related situations from the den or not far from the den. On the other hand, it is convenient for parent wolves to walk by the road, when they go for hunting and come back with food. Marking of borders of the denning area at the road seems to be also important for the parent wolves, and on such a road it can be done faster in this very busy time. Moreover, just along such a road alien wolves may come into the denning area. So, such terrain roads are very essential for wolves at breeding. Nevertheless, that does not mean that wolves like breeding close to a busy road. Such a road nearby the denning area may be quite small and rarely used by people, but anyway at the same time it is still the main road, which humans use to get to the wild area. Really big roads with intensive traffic and their adjoining areas are normally avoided by wolves. However, it is not always, and we recorded once pups staying 7–10 days in the pipe under quite busy road. In most cases, wolves choose a rather calm terrain road (approximately up to 60 visits per day) by which people come into the area. Having a lot of data on wolf denning in Belarus, we learnt that in most cases (76%) a wolf den was situated on the distance of 0.4–1.0 km from the main road in the terrain fragment that was chosen by breeding wolves for denning. Moreover, in many cases the denning area was situated on the distance of only 0.4–0.7 km from the main terrain road.

There is the wide-spread belief that wolf pups should be located at a stream or another source of drinking water. Actually, it is hard to reveal such a relation in our data on the wolf denning. In Belarus and adjoining regions, there are 0.4–0.7 km of natural streams (rivers and brooks) per one km^2 on average. Moreover, in the areas, where draining was conducted, the stream density is several fold (locally more than tenfold) higher than it used to be. Additionally, usually there are numbers of other sources of drinking water. Thus, there is so much water for wolves to drink that the mentioned feature of plausible den location is not useful, because water is actually available everywhere. The only excep-

tion are extensive sand dune areas with pine stands, where wolves breed rarely inside, but not rarely at the border. In a sand dune massif, breeding wolves indeed create dens not far from a stream or glacial lake, but it does not mean that such a den is situated one or two hundred meters from the water source. Parent wolves evidently avoid to situate pups in the close proximity of any waterbodies, because the surrounding is usually full of wild ungulates and people frequently visit these places. Both wild ungulates and people are dangerous for pups, and parent wolves know that very well.

Only during a severe summer drought (what actually became more usual in the last decades) presence of water source is getting an essential to place pups. So, with the climate warming this factor of presence of stable water source becomes more essential for placing of wolf litter in Belarus. Nevertheless, during early denning stage in May and June there is still a lot of water to drink the terrain-wide. It may be getting more important for wolves to have a stable water source in July-September.

While analyzing the ecological situation in the denning sites, we found that wolves prefer to situate their den in places where wild ungulates are not very active. These animals are a real danger for small pups (see Chapter 6), and parent wolves know that very well. Usually wolves follow this tactic quite strictly. Nevertheless, there may be exceptions. Once we discovered an open den at the roots of uprooted huge oak among swamped logging area, and there were many wild ungulates. The den was placed so high that it was unreachable even for an elk.

Despite of the fact that wolves avoid places with many ungulates for denning, at the same time, places with rich a prey supply(beavers and/or wild ungulates) need to be located close, optimally on the distance of 1–2 km.

Usually, during denning the breeding wolves avoid the places were brown bear or lynx are present frequently, at least, for the majority of cases. However, there may be some exceptions. For instance, once in Naliboki Forest we faced with the location of a brown bear hibernation den in the same 2 km^2 plot, where a couple of wolves placed theirearly days pups. This denning area was still used by the brown bear family until 25th of May, at least, whereas wolf pups were placed there since the last days of April till the mid-May. The distance between the centers of the denning area of the wolves and the brown bear family was about one km only. As to lynx presence, formulating general rules are quite complicated. When wolf pups and lynx kits are of early days, and both the mothers stay nearby the dens, the wolf den and lynx den may be very close. In one case we found that lynx kittens were placed in a former wolf

burrow on an island in a black alder swamp, and the distance between this lynx den and the nearest wolf denning site with two litters (a case of pack double breeding) was only about 500 meters. There was registered another such case, when in the large treefall, where already mother lynx with blind kittens was present, wolf family with blind pups has arrived. The distance between the wolf and lynx dens was about 350 meters, at least, for few days. When pups and kittens are older than 10 days and the mothers leave the litters alone and go for hunting, such a proximity of lynx den and wolf den is not characteristic.

As to denning itself, we would like to state that usually there are wolf denning sites including many dens (in our experience, it was up to 79), whereas a single den can exist from several hours to several days after giving birth. Parents relocate their pups from one den to a newly created one all the time, especially when there are too many mosquitos or the weather is rainy. Moreover, parent wolves worry all the time, and plausibly this nervousness also pushes parents to move their pups. Otherwise, it is hard to explain the many displacements of the litter. Normally, the new den, to where the parents move the pups (when that is motivated by the above reasons, but not because people scared the

(197, 198↑←) *Wolf pup that was abandoned by parents in the late August and it could persist till the mid-October. It found elk bones and tries to consume something from these remains.*

wolves), is situated fairly close to the previous den — from 3 m to 1.3 km, on average about 50 m (more often 10–30 m only). Mainly there are two basic types of wolf dens: an open couch-den and a burrow (see the various photos given before). The burrow-dens of wolves is reasonable to divide on two subtypes as a cavity-den and burrow-den. A cavity-den has merely a denning chamber, whereas a passage from the entrance to the denning chamber is absent or almost absent. In the case of a couch-den, the smaller pups are, the deeper and narrower such a den is. Such a narrow couch-den for early days pups may be called as a pit-den. So, again couch-dens may be divided into two subtypes of a pit-den and a couch-den. A deep pit-den of 25–40 cm in the diameter (e.g. see Photo 171) keeps the pups together, saving their warmth and prevents them from creeping around. Sometimes even in the beginning of their denning breeding wolves do not create such a pit-den, whereas they make a larger den (some kind of a couch) with scratched floor. It is approximately 60–100 cm long by 40–70 cm wide (e.g. see Photos 76 and 79). Quite often breeding wolves create a burrow by enlarging a badger sett or red fox earth, or sometimes a beaver burrow. The wolf part of such an enlarged burrow extends for up to 5.2 m and in case of a relatively long wolf burrow it ends by a chamber of 45–70 cm in diameter. The diameter of the wolf burrow passage is usually 30–40 cm. From the denning chamber of wolves, a markedly smaller initial passage goes up (*i.e.* from former badger sett or red fox earth), where pups can hide (Photo 105). In peat and sand, fairly often wolves dig entirely their own burrow, usually 1–3 m long with a chamber in it. All breeding wolves use open dens, but not all

(199, 200↑↓) *Lonely persisting wolf pup that was abandoned by parents in the late August.*

(201-205↑→) *Digging of red fox earths by breeding wolves. Usually one of them is digging, while another wolf ambuscade in a close proximity. Deep digging into the earth disturbs the vixen a lot, and finally it tries to escape. Another wolf in ambuscade overtakes the escaping fox and kills it. Usually carcass of such a red fox that was killed by breeding wolves remains 30-100 meters from the destroyed earth.*

(206→) *Female red fox that was killed by wolves.*

of them dig burrows. Some of them produce many burrows (30–50 burrows, in particular, if they stay in abandoned peatery), whereas others only dig some entrances in badger setts and burrows of red foxes.

Both members of the breeding couple (*i.e.* the male and female) create dens. The digging activity of the breeding wolves begins 5–21 days before parturition, whereas in most cases it happens about ten days before that. So, finding a wolf burrow does not mean that there are already pups nearby. Small open dens in kind of small pits suggest either there are already pups or they will appear in a few days maximum. However, such a pit with a worn down look says about the presence of pups.

Fairly often parent wolves do not use the created burrows in May and the first half of June. Only later in July–August, such burrows may be used a lot; in particular if it is either too rainy or too hot, or if there are too many mosquitoes. Sometimes in June–August, wolf litters stay for many days in and around badger setts with enlarged entrances.

Another important question is what the possible distance between neighboring denning areas with different litters. It makes sense to consider this parameter, if the neighboring packs overlap in their home ranges. Otherwise, in the conditions of a low population density in wolves, neighboring packs may be too remote from each other. By other words, it means that the wolf number is markedly lower than the potential level at the habitat carrying capacity. However, if the number of wolves was at the level of habitat carrying capacity that in this case in Belarus litters of actually neighboring packs were for 6–24, mean 16.7 km apart from each other.

Nevertheless, there may be many various peculiarities in the breeding of such neighboring packs, and wolf litters may appear on markedly different distance. It may happen that in the neighboring pack there is no litter at all. One of the reasons for that may be that the dominant female is sterile. Another cause may be that the pregnant female was killed by hunters after the mating season, for instance in March, and this frequently happens. On the other hand, there may be two or even three litters in one pack, for instance when the founding male (the father) mated with daughters too. In last situation, the litters may be situated within a small distance of 0.4–4.2, mean 1.2 km apart.

While investigating the effect of several external factors on the wolf denning behavior with the data of Table 4.1, we found that the number of mosquitos, rainy weather and disturbance by human drive the complexity of denning behavior in wolves. Under disturbance by people we mean not only human activity against

wolves and their habitats, but also just human presence in wolf habitats what is already a disturbance. With increasing the above factors, a higher number of dens was used by parent wolves: rain with total number of dens (r_s=0.38, P=0.04); mosquitos with total number of dens (r_s=0.42, P=0.02); disturbance by people with total number of dens (r_s=0.52, P=0.004). Besides, the disturbance by people (mostly indirect disturbances like logging activity) leads to more used denning plots (r_s=0.68, P=0.00004) and longer distances between the denning plots (r_s=0.46, P=0.01).

One of the interesting behavioral features of breeding wolves is that parents deliberately abandoned some pups to die, while relocating the litter from one den to another one. During our long-term experience of searching for wolf pups, we discovered several times such abandoned pups on the recent den: one abandoned pup (n=5), two pups (n=2), and once there were four abandoned pups. In most cases, the abandoned pups were dead. In one case one pup was killed by one of the parents. For all these 8 cases of leaving some pups on the former den, the parent wolves still had other pups alive that were tended by them. Normally this deliberate left of a few pups to die happened, when the litter was large (consisted of more than 7 pups), perhaps, too large for the wolf breeders. We recorded this in 5 out of 6 cases, whereas in 2 cases the number of pups was unknown. So, perhaps, this strange behavior of parent wolves having many pups (*e.g.* 8-12) is motivated by their feeling of inability to raise so many of them.

There is suggested by Mech & Boitani (2003) that a young mother may abandon her litter, first of all, in case of a multiple breeding in the wolf pack. In our experience with wolf breeding we did not face with this feature. In the above-mentioned 8 cases of a deliberate abandoning a part of the pups by the parents, for 7 cases we know the mother's age approximately. Only one mother was young (two years old). The other six mothers were older than 3 years; two of them were killed by hunters later during the next winter, and we determined their ages precisely (4+ and 6+).

The above-mentioned cases of left pups without care to die relate to early days pups. This is a more or less common phenomenon for breeding wolves. However, even older wolf pups may be abandoned by their parents. In the mid and late summer of 2013 in Naliboki Forest we faced with that for several times. The stories were as follows. During the quite long period of 1999 till the spring 2013, the wolves lived in the conditions of a high density of medium-sized (and thus not risky) prey: roe deer - on average 398 inds per 100 km^2; wild boars – on average 234 km^2; and beavers – 847 inds per 100 km^2. It seemed that they

Table 4.2. Diets (%BC) of wolf pups and their parents in Naliboki Forest in diffrent localities and years

Food item	Kupalishcha, 2004		Kupalishcha, 2005		Kupalishcha, 2011	
	pups	parents	pups	parents	pups	parents
Small mammals sized up to muskrat	1.0	0.7	–	0.5	6.5	–
Hares	5.9	5.1	8.5	7.8	–	2.7
Raccoon dog, red fox, badger	1.9	2.1	0.6	2.1	–	0.9
Beaver	44.7	39.2	40.4	13.9	56.1	28.9
Roe deer	18.3	19.5	10.5	17.8	28.3	49.0
Red deer, elk	10.0	7.1	9.5	11.6	6.1	9.2
Wild boar	14.5	22.6	12.1	35.0	3.0	8.5
Birds, mostly tetraonids and ducks	1.0	0.7	2.8	3.5	–	–
Domestic dog	0.7	1.0	–	0.5	–	–
Domestic ungulates	0.6	0.8	14.4	6.2	–	–
Plant matter	1.4	1.2	1.2	1.1	–	0.8
Number of scats analyzed	174	157	169	120	39	67

were 'spoiled', being able to only foraging these relatively easy-catching prey, and they almost did not hunt bigger (and thus more risky) elks and even red deer (Sidorovich, 2016). Perhaps, at that time the local wolf population in Naliboki Forest even lost good skills to hunt this bigger prey as an elk. During February-July of 2013, these medium-sized preys declined greatly. An extremely long-lasting and abnormally snowy end of winter in 2013 impacted the populations of the wild boar and roe deer dramatically. More than 80% of the wild boars and more than 90% of the roe deer died in March and April. Then in June and July most wild boars, which survived through the harsh early spring, died from a hard disease. The summer of 2013 was rainy and beavers were not so easily available to hunt as usually. In these conditions, the efficiency of foraging by parent wolves declined strongly and therefore they refused their litters even so their pups were already 2-4 months old. We guess that 7 out

Table 4.2 continued

Food item	Kupalishcha, 2012		Kaliuhi, 2010		Kaliuhi, 2012	
	pups	parents	pups	parents	pups	parents
Small mammals sized up to muskrat	6.2	–	6.7	–	6.2	0.4
Hares	3.7	–	–	–	1.6	–
Raccoon dog, red fox, badger	–	–	–	–	–	–
Beaver	50.1	37.5	46.7	18.2	58.4	49.3
Roe deer	16.2	19.5	26.8	51.5	21.5	22.7
Red deer, elk	2.4	11.2	–	–	–	6.7
Wild boar	20.2	30.4	19.8	30.3	12.3	19.4
Birds, mostly tetraonids and ducks	0.4	–	–	–	–	–
Domestic dog	–	–	–	–	–	0.9
Domestic ungulates	–	–	–	–	–	–
Plant matter	0.8	1.4	–	–	–	0.6
Number of scats analyzed	58	51	30	33	58	92

of 11 present litters were abandoned to die during that summer of 2013 in Naliboki Forest (Sidorovich, 2016).

However, we could only learn the stories of two such litters precisely. One of the litters, which in May consisted of 5 pups, was left to die in the beginning of August, when still there were 3 or 4 pups. These pups starved, but persisted 15-20 days (at least, 1-2 of them survived so long), then they died. Another wolf litter, in which initially there were 7 pups, was abandoned late August. The pups were already big enough to forage something small themselves, and they hunted small rodents on the large grassy opening, where they stayed. By the lucky chance, the late summer and early autumn of 2013 were characterized by a high abundance of voles of the genus Microtus on the grassy openings, and 3 pups survived themselves for long till the beginning of October, when they were accepted by their parents again. Nevertheless, the food shortage suppressed their growing, and

Table 4.3. Diets (%BC) of wolf pups and their parents during the period of July-mid September in Naliboki Forest in diffrent localities and years

Food item	Hala Balota, 2007		Hala Balota, 2008		Hala Balota, 2009		Hala Balota, 2011	
	pups	parents	pups	parents	pups	parents	pups	parents
Small mammals sized up to muskrat	2.4	1.4	0.9	0.6	–	0.5	16.4	1.0
Hares	0.3	0.7	4.8	1.1	–	–	–	0.9
Raccoon dog, red fox, badger	–	2.8	–	2.2	–	0.6	–	0.4
Beaver	60.4	29.6	44.2	17.4	83.6	32.9	46.7	39.6
Roe deer	10.7	21.0	21.2	29.3	2.4	34.9	32.3	29.3
Red deer, elk	13.4	29.5	–	18.2	–	6.8	–	9.7
Wild boar	8.9	10.5	28.1	26.4	14.0	18.4	3.6	14.4
Birds, mostly tetraonids and ducks	–	0.9	–	–	–	–	–	0.4
Domestic dog	–	1.4	–	4.1	–	3.7	–	08
Domestic ungulates	2.5	1.2	–	–	–	1.0	–	1.6
Plant matter	1.4	1.0	0.8	0.7	–	1.2	1.0	1.9
Number of scats analyzed	69	175	66	136	40	92	45	74

even in March of 2014 they were rather small compared to a normal almost yearling wolf.

On the other hand, some parent wolves tend about already dead pups (even decayed ones), by carrying them from one den to another, together with alive pups. Such a behavior by parent wolves was recorded by us for three times. These three litters on the moment of their finding consisted of 5 alive pups and one dead pup, 7 alive pups and one dead pup (already bad smelling), and 3 alive pups and 4 dead pups.

Stealing pups by mothers from each other in a case of pack multiple breading is another pattern of unusual denning behavior in wolves. They steal not all the pups; usually only 1-3 pups are taken from another litter. In our research experience and the practice of three other wolf pup searchers (altogether about 160 wolf litters that were looked through) such a denning behavior was registered for six time. In the respective litters, we recorded normally developed

Table 4.3 continued

Food item	Shubin, 2011		Shubin, 2012		Sviaty Kalodziezh, 2012	
	pups	parents	pups	parents	pups	parents
Small mammals sized up to muskrat	13.1	–	2.5	–	2.8	–
Hares	1.1	0.6	–	2.0	2.2	2.5
Raccoon dog, red fox, badger	–	1.7	–	–	–	0.4
Beaver	37.0	29.3	54.0	28.9	63.3	45.6
Roe deer	26.5	30.9	19.5	27.7	11.1	12.4
Red deer, elk	2.3	7.9	3.5	4.8	–	6.9
Wild boar	19.3	27.5	17.8	36.2	20.0	31.3
Birds, mostly tetraonids and ducks	–	–	2.3	–	–	–
Domestic dog	–	0.5	–	–	–	–
Domestic ungulates	–	0.7	–	–	–	–
Plant matter	0.7	0.9	0.4	0.4	0.6	0.9
Number of scats analyzed	67	59	77	80	85	64

pups of clearly different ages. These mixed litters consisted of 3 and 4 pups of distinctive ages; 4 and 1; 5 and 1; 3 and 2; 7 and 1; 5 and 4. So it is clear that in such a case the wolf litter consists of bigger and smaller pups. Sometimes, this size difference may be too big, and bigger pups suppress the smaller ones. Such a suppressed small pup dies somehow, finally being trampled in the den bedding materials. Twice we faced with such a case of dead pups in the mixed litters. In one of those wolf dens we found 2 small alive ones, one small dead pup and 4 markedly bigger pups; whereas in another case - 3 small alive, 2 small dead and 4 markedly bigger pups.

One of the common behavioral patterns of denning wolves is the persecution of red foxes. Particularly wolf breeders kill vixens at their denning earths. Usually one of the parent wolves is digging the red fox earth, while the other one is lying in an ambuscade in a close proximity of the red fox earth. This deep digging into the burrow

disturbs the vixen greatly, and finally she tries to escape. The wolf waiting in ambuscade overtakes the escaping vixen and kills her. Usually the vixen carcass remains 30-100 meters from the destroyed burrow. As to the badger and raccoon dog, killing of them during denning period at their dens similarly as in the case of the red fox is not so common.

One of the specific features of the wolf denning behavior is finding a new partner very fast, when one of the mates died (or was killed). We learnt this by several anecdotal stories, but four of them we got know in a very detailed way and were partial evidences. These stories may be briefly told as follows.

Story 1. In early June, still a bit lactating female wolf was trampled by six caws in a grassland at a homestead in Naliboki Forest; the pups survived somehow, and locals from the homestead registered presence of wolf pups on the distance of 1-2 km away during the whole warm season (pup howling, footprints etc.); in early November just in that same place a wolf pack was killed; the pack consisted of three pups of the year (one of them was markedly bigger than the other two pups); two big males (one of them, perhaps, was the pups' father) and one adult female ('step-mother'). Perhaps, the step-mother appeared quite soon, otherwise so small pups could not survive. We think that it was a case of multiple breeding in the wolf pack, and the step-mother was the mother of another litter, because the killed pups were much distinctive in their sizes.

Story 2. In Paazierre Forest in the mid-June a big male bringing food for its mate with pups was killed at a pathway to the denning site; the mother was slightly wounded in the hind leg, and it begun crippling; in 5-7 days a new big male appeared with the crippling mother; in the early July this step-father was killed; the female was still crippling; it got the new mate within 10 days; in December all of them

. the pair of the mother and second step-father and 4 pups of the year were killed more or less in the same area.

Story 3. In the late May in Paazierre Forest a big male wolf and a lactating female wolf were killed; then in about 3 days several adult wolves walked there again; in the mid-August in the same place (wolf pathway) five wolves were killed; the killed wolves were an adult female and 4 normally developed pups of the year of greatly different sizes; the next night at the same pathway a big male wolf and a pup were killed again. Afterwards in 9 days an adult female and male wolves and three pups were observed in the place proximity again. We guess that it was a case of double breeding in the wolf pack with quite fast getting of a new mate, when the previous partner was killed.

Story 4. In Paazierre Forest in the early August two adult wolves with 5 pups of the year were observed; one big adult male and one pup were killed, while the others escaped; in 10-15 days the two adult wolves and 4 pups were seen, while walking more or less in the same area; in early December a pack of 6 wolves was eliminated there; there were 2 pups of the year, one adult female (perhaps, the mother), big male (step-father) and two more males that look like yearlings.

At the end of this item, we would like to conclude with the main results of the denning studies. Defining under the wolf breeders at the denning stage one or several pregnant females with an adult male or sometimes several males, our results suggest that for the most of the investigated situations during the denning periods breeders send away the rest members of the pack (mostly yearlings), at least, for two months. In this case yearlings stay on the distance of 3 to 8 km from the breeders.

Denning in wolves takes place in several denning sites (up to four) that are situated on the distance of 2 to 7 km from each other. In each denning site there are usually from 10 to 30 dens (mostly open couches and few burrows), between which pups are relocated by the parents. Usage of each den is not long and lasts from several hours up to 3 days mostly. The choice of the denning site is determined by sheltering features of habitats, presence of wild ungulates as few as possible, absence of aggressive lynxes, good habitats for foraging not far away and proximity of the main road in the area chosen for denning. The number of mosquitos, rainy weather and human presence drive the complexity of denning behavior in wolves. The increasing of these factors leads to higher number of dens that are used by parent wolves.

4.3. Raising of pups after weaning

After the busy period of denning, when early days pups mostly eat the mother milk, a new and markedly different situation in the wolf family starts. The pups need milk less and less and begin to consume some solid food, mostly meat brought by the parents in their stomachs. The pups become more and more mobile and that increases the mobility of the parents.

At this situation some interesting questions need to be raised. At which age of the pups does the lactation start to decline? At which age do pups begin to eat solid food? At which age of pups does the weaning happens? We did not find any substantial publication related to the questions for wild-living wolves in the European forest zone.

Of course, there are many published articles on the questions in relation to wolves in captivity, but those may only suggest

some hypotheses for the wild animals. So, these answers still need to be answered for wolves in the wild.

Of course, there are a lot of studies conducted on these questions in North America (Mech & Boitani, 2003 and references therein), but the American and European wolves are greatly different. They are like different species in many of their characteristics, particularly behavioral traits. Again, it may suggest something, first of all, to establish hypotheses to study on the questions in Eurasia.

How is it possible to investigate such complicated questions in the wild? Telemetry? We did radiotracking (both VHF and GPS GSM) on twelve predator species and know very well, what the method can, but also what it can not. We disagree, when researchers read too much from the telemetry signal sequences with some inspection in the wild. Perhaps, here in Europe, where wolves are so shy, it is possible mostly doing study on sporadically gained carcasses of recently killed adult wolves and pups in the respective seasonal period, by gathering data long-term, what we actually did.

Thus, we would like to conclude that these quite important questions of the wolf reproduction are still poorly known in the European forest zone. We gathered not a lot of data on the questions and mostly it is sporadic data. Anyway, nevertheless this something is worthwhile to describe.

We used two kinds of gathered data. First, for nine times in the period of the mid-May-June we faced with situations, when pups of known age (they were found by us at dens before) ate solid food, mostly meat brought by parents in their stomachs. Another source of information were the carcasses of wolf mothers (n=6) and pups (n=89), which were killed by hunters in the period of May till the mid-July. In half of these cases we knew more or less the age of the pups (*e.g.* before the pups were killed by a hunter we found the den with the pups of early days) .

These irregular data suggest that the duration and importance of the lactation depends on the food base. While comparing a few cases in the conditions of very rich and poor prey supply, the duration the of lactation by wolf mothers was almost double different. We evidenced that for pups of about 40 days old the mother's milk was already not so important in the conditions of rich food base and the mother secreted milk only a little bit. But, when prey were scarce, pups of almost 70 days old were nursed and the mother was still strongly milk-secreting. The killed pups had meat in the stomach since the age of 20-25 days old, and the stomachs of pups of 40-60 days old rarely contained milk and were filled with meat.

With finishing the lactation phase, a wolf family starts moving markedly more *i.e.*

more often and on longer distances each time. While adverting to this period in wolf families, researches frequently use the term of a 'rendezvous site' and distinguished this from a resting site (*e.g.* Theuerkauf *et al.*, 2003). The authors defined 'rendezvous sites' as places, where young wolves stayed for several days and to which the adults returned regularly, and resting sites as places, where wolves rested once for an hour or longer. We evaluate these different definitions as too sophisticated, and avoid to use them. In our quite big dataset (47 wolf families were more or less followed during summer) we faced with the following. Sometimes, wolf parents left the pups shortly in a particular place, came back and picked the pups up. It is something negligible, and it does not mean that it should be named somehow with a particular term. Indeed, nobody terms a random place, where a wolf defecated once. We think that such a short stay of pups in a particular place means that something was wrong with the choice or the family was making a too long displacement. Other places, where parents leave their pups, were used longer and in such a place parents spend much time (hours) every day. Fairly often parents rest few hundred meters away from this pup locations, controlling the situation around the litter and avoiding disturbance from too active pups. Well trampled resting couches of parents indicated this habit many times. So, both rendezvous and resting sites occur altogether, and we assume that it is quite reasonable. We call such a place the wolf family homesite.

In July-September we found the wolf family homesites (n=139) in the following habitats or microhabitats:

(1) High grass stands with some bushes or without any bush usually on abandoned drained lands (mainly at drainage canals with wolf burrows in canal banks) – 18 (15) times, 13(11)%;

(2) Willow bush thickets – 7 times, 5%;

(3) Large treefalls – 15 times, 11%;

(4) Some treefalls in an old spruce forests – 24 times, 17%;

(5) Fern stands in young forests – 9 times, 6%;

(6) Wolf burrow sites, i.e. where several wolf burrows are situated in a small area up to 10 ha, it includes former badger setts with enlarged entrances; usually such wolf burrows were created in sheltered biotopes (quite often that was in abandoned peatories) – 19 (11) times, 14(8)%;

(7) Logging areas with a lot of tree remnants and early reforestation – 23 times, 17%;

(8) Rye fields – 2 times, 1%;

(9) Big haystacks (in that single case the big (about 30 meters long and 7 meters wide)

(207, 208) *Mother (above) and father (below) are bringing meat food in stomach to their pups.*

(209↑) *Father is regurgitating meat from stomach for pups.*

(210↓) *Bringing food for pups in muzzle.*

haystack from the last year that was situated at the forest edge) – one time, 1%;

(10) Thickets of grass and dead tree material in abandoned beaver settlements; there were many beaver burrows in such places – 17 times, 12%.

(11) Young spruce thicket with some open spots - 4 times, 3%.

Taking into account possible factors and wolf demands for a family homesite, we noticed that all of them were well sheltered somehow. When there were plenty of mosquitos, the homesites of 1, 6, 8, 9 and 10 were mainly used by wolf families. During rainy weather the homesites of 3, 4, 6 and 10 were used more frequently. In the pup raising period after the weaning phase, the distance from the wolf family homesite to the nearest road and the frequency of wild ungulate presence in the homesite were not important in contrast to the denning period. As to presence of people (*e.g.* collectors of mushrooms or berries), we noticed that the influence was a particular family-related, because we found so different patterns of homesite location in relation to human disturbance. Once, parents immediately reacted on our visiting of their homesite by escaping with pups during the first night, whereas the others persistently stayed in the same well-sheltered homesite despite of the repeated visits of us and mushroom collectors. Actually, the first pattern of such a response was usual, while the second one was registered for three times only. In two situations there were young spruce thickets with some fallen trees and several wolf burrows, and in one case it was an extended treefall.

It is interesting to know how long a wolf family may stay in a given homesite. Checking that with howling and camera-trapping, we are sure that it may be quite long. In one case, the wolf family stayed in a few hectares plot within tall grass stands at drainage canals for two months, at least. Another such case of about two months stay of wolf family with pups was documented on the relatively large forested island in the place of small river split. Spruce forest with several glades were mainly used by the wolf family on the island. Moreover, this island was regularly visited by the wolf family till mid December. Another similar case, but this time in the mosaic of grass stands and willow bush thickets at drainage canals, the wolf family stayed about 40 days. Another long stay of wolf family was detected in extended treefall (five neighboring treefalls in the area of about 40 hectares), where the family lived from the denning in the late April till the end of September, *i.e.* five months. However, usually (more than for half of the cases) wolf families used homesites for 5-12 days only.

We analyzed pup diet compared to their parents diet in the period from mid-July till

mid-September. We could not collect scats of pups earlier than from the mid-July onwards, even when we knew the particular place of their stay. In June and quite often till the mid-July the majority, (sometimes all) scats of pups are collected by their mother, and perhaps by both parents. Parents carry the pup scats in their stomachs (like in a bag) away, where they drop all of them by vomiting. We occasionally learnt this in Paazierre Forest in the late June of 2003, when a mother wolf was killed by a hunter from a hide in the proximity of the den. There were pup's excrements in its stomach. We immediately realized that was the reason, why we could only find some scats at the wolf homesite with pups. Later in Naliboki Forest, we discovered wolf vomiting twice with many scats of pups, and we easily recognized it.

Such comparative dietary studies were carried out for 13 litters and their parents in 2004-2012 in Naliboki Forest in the localities of Hala Balota, Kupalishcha, Shubin, Kaliuhi, Sviaty Kalodziezh (Tables 4.2 and 4.3). It should be noticed that in those years, food base for wolves in Naliboki Forest was very rich. Looking at the data, the most distinctive feature of the pup diet is the markedly higher portion of beavers compared to that in the parents diet – in 1.2-2.9, mean 1.9 fold. Most of the differences are statistically significant ($G>31.2$; $P<0.02$). Also, pups ate quite a lot small rodents, catching them themselves. Therefore, the small rodent portion in the pup diet was essential for 6 out of 13 litters studied (Tables 4.2 and 4.3).

Approximately, in the beginning of October pups start walking with their parents most of the time, however, still may be left for some time in a sheltered place. Since late October or early November pups follow their parents all the time.

4.4. Some behavioral traits of wolf-stray dog pairs at denning and raising pups

In Naliboki Forest we had the possibility to also trace the breeding behavior and raising of the pups by two wolf-stray dog pairs. These stories are worthwhile to tell.

The first story is as follows. During late autumn at the boundary of Naliboki Forest in the surroundings of a cattle farm and village we detected a pair of stray dogs. They mostly hunted small rodents and scavenged around the cattle farm and in the rubbish dump of the village. Mainly they avoided interactions with people, were mostly active at night, so it was hard to observe them. Quite often they rested in the forest on the distance up to one km from the village. The dogs marked three terrain roads that coming from the village to the forest. The stray dogs lived there between the cattle farm and village rubbish dump till the end of January, when the

male dog was killed by a wolf or a pack of wolves. One of the workers of the cattle farm looked through the spot of the kill. There were remains of the male dog only, whereas the female dog had disappeared. In April a few locals from the village observed a strange pair: a big wolf and a medium-sized dog on the road not far away from the cattle farm. In early June we noticed that there was like a wolf and dog pathway coming from an abandoned peatery to road. Searching for a den of the possible wolf-dog pair, we discovered the den in a few hours. The den was a burrow with several entrances (enlarged former red fox earth), which was situated in a big peat mound that was densely overgrown with raspberry and blackberry bushes. On the distance of about seven meters from the den, we were horribly attacked by the mother dog. It was the same female dog as the one that lived with the killed male dog. The mother dog chased us for about 200 meters, but we were not wounded defensing ourselves by axe and a big wooden stick. There were three repeated attacks during these 200 meters that we were gradually retreating. At the den we only noticed one rather big pup (about 2 kg) and there were a lot of feathers from poultry (mainly from chicken and goose) around. Later we learnt that in the village chicken and goose disappeared one by one; perhaps, the mother dog visited easily the village and killed poultry. Here it is worthwhile to notice that in Belarus it is common that in villages dogs that are freely walking on streets are common; nobody knows all the dogs in a village and nobody chases them. In August-September the wolf-dog pair began to attack cattle in the daytime, mainly young horses and adult caws to get an udder. Hunters tried to kill the wolf-dog pair, but only three other domestic dogs were randomly killed in the village surroundings. In December, while censusing wolves, we faced with a pack trail consisted of one trail of a big wolf and four dog trails. It was on the distance of 4 km from the cattle farm. There was no doubt that the trails belonged to the hybrid family. They stayed there till February on the area of about 220 km^2. They marked the area a lot, may be even more that an average wolf pack. Just before mating season in wolves they had disappeared. We heard something about that hunters killed some dogs in forest in that area, but we are not sure that it actually happened. Even if that was the case, we are not sure that all the individuals from the hybrid pack were actually killed. That is all we know about the wolf-dog couple. We would like to add that the food base for wolves was rich and the wolf density was rather high in Naliboki Forest that winter – 2.3 inds per 100 km^2.

Another story of a wolf and stray dog pair took place in the center of Naliboki Forest. Prey supply for wolves was moderate, and

the wolf population density was 1.4 inds per 100 km^2 (so, wolves were not rare). In a hamlet only one house was occupied by a man, who was ill on alcoholism. The man has a female dog that looks like a Siberian lajka. The dog was ranging free in the hamlet proximity for most of the time. She was smart to hunt something, and according to the owner's words sometimes she brought a roe deer, beaver or hare on the yard. Once this dog killed our domestic red fox and ate it entirely; merely the fox tail and radiocollar were left on the spot of the kill in the hamlet surroundings. Nevertheless, fairly often the female dog was keeping on the chain leash at her cabin. Once in the late autumn the man started drinking alcohol too much and continuously. The female dog was not fed anymore for long. The man was so kind that released the dog from the leash before he went on the hard booze. In a month, the man was taken to a hospital. The female dog survived and even succeeded to support with food her two male pups of the year, which mostly continued to stay on the abandoned yard. In mid-January the female dog was registered living with a big male wolf; in the hamlet surroundings we found many wolf and dog paired trails and the pair was observed for several times. They mainly hunted roe deer and beavers and lived together till May. The pair visited the hamlet and brought some food for the two dog pups. They looked not starved. The female dog gave the next birth somewhere in the forest in mid-April and on the 22nd of April she relocated the new pups to the owners yard. There, it dug a deep and broad burrow under the shed base close to her cabin. Also, the pups were placed in several open couches at the shed. The male wolf regularly visited the abandoned hamlet at night and fed the mother. During that time the yearling dogs were chased from the hamlet, and they ranged in the neighboring village on a distance of 13 km apart. Suddenly the owner came back to the house; he accepted the pups and they were taken by other locals as well. The female dog still walked free, and not seldom we registered their paired trails of the male wolf and female dog on sand roads in the proximity of the hamlet. Till March of the next year, the female dog ranged with the male wolf. They produced a lot of territorial marking and regularly visited the former owners yard. At that time, the man sold the house and moved to the neighboring village. In the late March the man captured the female dog on the yard and moved her to the village. Being on the chain leash, she gave birth again in the new cabin of the new house of the owner. The male wolf seemingly disappeared. We did not follow the story anymore.

Chapter 5. Fertility and reproduction regulations in wolves

There are many studies available on the fertility in grey wolves and the species breeding in the demography aspect (*e.g.* Bibikov, 1985; Mech & Boitani, 2003 and references therein; Mech *et al.*, 2016). Regionally, in Belarus and neighboring countries (Poland, Lithuania, Latvia, Estonia, Ukraine, the western part of European Russia, so, in the extended area of the wolf range in Europe) fertility in wolves was poorly investigated before our given study. Of course, the litter size in many of these areas was known, but it is only one of the important characteristics of the species breeding. The other important characteritics are frequency of breeding in females; the age of sexual maturity; fecundity as number of non-resorbing embryos per a pregnant female, and frequency on embryos resorbing. Moreover, it is only half of the job to assess all these parameters. It is strikingly important to get to know whether there are density-dependent regulations of the above breeding characteristics or not. Also, the dependence of these characteristics on food base should be checked.

Density-dependent regulations of the wolf reproduction within the whole species range in North America and Eurasia were almost not registered. Only the study by Mech (1975) reported that the proportion of females amongst pups increases for low-density population of the species, what potentially can provide a higher reproduction rate. In the published studies more frequent breeding of female wolves as well as the cases of double and triple breeding in wolves were mainly connected with a rich prey supply and these phenomena were not related to the declining of the wolf population density because of the absence of such evident trends and respective data (Mech & Boitani, 2003).

During our long-term study on the wolf reproduction in Belarus (some study since 1985) we revealed and well-documented all possible ways of density-dependent regulations of wolf reproduction such as more frequent breeding of females of two and more years old; pack multi-breeding (mostly double, sometimes, triple-breeding in a pack); fecundity increase with biased sex-ratio in pups, early breeding of females of one year old; and hybridization with stray dogs. Quite opposite to the early studies (Mech & Boitani, 2003 and references therein) in our data we did not find much support to the idea of higher breeding efforts in wolves in the conditions of a better prey supply in Belarus.

Table 5.1. Portion of pregnant adult female wolves in the period of March till the mid-April, Belarus, 1985-2014 (mainly 1989-2008), n - number of adult females that were investigated

Population density, inds per 100 km^2	Poor supply with prey	Moderate supply with prey	Rich supply with prey
Low, <0.5	91%(n=21)	90%(n=20)	94%(n=52)
Medium, 0.5-2	95%(n=19)	81%(n=26)	95%(n=20)
High, >2	77%(n=30)	82%(n=22)	69%(n=48)

5.1. Frequency of breeding in female wolves and its density-dependent variation

In Belarus, about 84% of pregnant females amongst 255 females of about 2 years old and older were registered, which were checked in March till mid-April (the long-term sampling of 1985-2014, mainly in the period 1989-2008). Only one out of 169 young females (almost one year old), which were checked by us in March till mid-April, was pregnant so early.

Table 5.1 represents the above mentioned data on pregnancy of adult females (almost 2 years old and older) in relation to the various prey supply (poor, medium and rich) and the level of wolf population density (low, medium, high; see the range in the table). For the majority of the cases (more than 90%) there were noticeable embryos in the females' uterus. At the same time, the reproductive organs of some of the adult (about 2 years and older) females were characterized by still estrus (the last registration was on 11th March) or very early embryogenesis with an increased utero having relatively developed blood-vessels (Danilov et al., 1985; Kreeger, 2003). Such females without evident embryos, but with these other clear features of breeding were registered as plausibly breeding ones, but there were not many of them (n=12).

The parameters to assign the categories 'poor', 'moderate' and 'rich' prey supply, are as follows. The poor one is characterized by a low density of wild ungulates (usually there were fewer than 10 elks, 60 wild boars and 40 roe deer per 100 km^2, no red deer, and a relatively low or medium density of beavers, which is less than one settlement

per one km^2). A rich prey supply means that there were more than 100 elks and red deer per 100 km^2 altogether, more than 120 wild boars and 180 roe deer per 100 km^2 and at least 2 beaver settlements per one km^2. So, the moderate prey supply for wolves in Belarus during the period of the given study was situated between the poor and rich ones.

The data given in Table 5.1 suggest that in Belarus, the portion of breeding female wolves was quite irrespective of prey supply. Indeed, there is no evidence between either the respective estimates in Table 5.1 or for the material that is taken altogether irrespectively of the level of population density for the situations of poor, moderate and rich supply with prey: 86%, 83% and 84%, respectively.

On the other hand, the portion of breeding female wolves is strongly depended on the wolf population density: low population density of wolves – 93% of pregnant adult females in the period of March till the mid-April, medium – 89%, high – 74% (the differences are statistically not significant).

With the exception of the one breeding yearling female (10-11 months old), which was registered amongst the investigated carcasses of female wolves (see earlier), we know about two more cases of breeding by yearling females.

One case of this early breeding of one yearling female was registered by means of

Table 5.2. Number of non-resorbing embryos in pregnant adult female wolves in the period of March till the mid-April, Belarus, 1985-2014 (mainly 1989-2008); min-max(mean), n - number of pregnant females that were investigated

Population density, inds per 100 km^2	Poor supply with prey	Moderate supply with prey	Rich supply with prey
Low, <0.5	2-13(8.7), n=18	4-11(8.9), n=15	4-13(8.4), n=46
Medium, 0.5-2	3-8(5.5), n=18	2-12(7.2), n=20	5-9(6.1), n=17
High, >2	2-11(6.2), n=21	2-9(5.0), n=17	3-10(7.0), n=30

marking with finger clipping and track checking in Naliboki Forest in 2001. In the mid-July this young mother lost the litter.

Another case of breeding of a yearling female was found in Paazierre Forest in 2003. During the last days of January, the majority of individuals in a big pack of wolves including founding female were extirpated; only a big male and two other markedly smaller individuals survived. Nevertheless, in May 2003 there were pups in the pack core area; then in the mid-June the mother was shot; it was aged precisely as 1+, actually 13-14 months old.

So, we found a quite high portion of adult female wolves that breed – about 84%. Also, our data suggest that the frequency of breeding females depends on the species population density (the lower the density, the more females actually breed), but this reproduction parameter does not relate to the prey supply. When the wolf population density is low, the majority (93%) of adult females (age 2 years and older) breed, and even some of the yearling females breed.

By analyzing the collected data on the frequency of breeding by female wolves, it is worthwhile to mention that it happens sometimes that a heavily pregnant female wolf dies in the last 10-20 days before parturition. Pregnant females are relatively weakened and clumsy and stay alone quite

Table 5.3. Indices of wolf abundance (number of trails per 1 km of transect daily, and winter number of wolves per 100 km^2 estimated by game wardens), number of wolves killed in Paazierre Forest, northern Belarus, 1988-2003

Year	Wolf trails per one km daily	Estimated density per 100 km^2	Number of killed wolves
1988	?	?	50
1989	?	?	50
1990	0.6	2.2	64
1991	0.5	1.3	66
1992	0.6	1.5	80
1993	0.3	0.9	42
1994	0.3	1.6	34
1995	0.9	3.6	38
1996	1.6	2.1	74
1997	1.2	3.0	62
1998	0.4	0.5	64
1999	0.2	0.8	61
2000	0.2	1.7	54
2001	0.4	0.5	35
2002	0.4	0.7	40
2003	0.5	1.9	36

Table 5.4. Wolf breeding data based on den findings, Paazierre Forest, northern Belarus, 1985-2003

Year	Number of pups	Average number of pups	Number of female pups in each litter	Number of male pups in each litter	% of females among pups in each litter	% of females among all pups investigated
1985	3 5 9 7 6	6.0	3 2 4 4 3	0 3 5 3 3	100 40.0 44.4 57.1 50.0	53.3
1986	8 8 4 5	6.3	5 4 2 2	3 4 2 3	62.5 50.0 50.0 40.0	52.0
1987	5 6 3 7	5.3	3 3 2 3	2 3 1 4	60.0 50.0 66.7 42.9	52.4
1988	7 4 5 5	5.3	? 2 2 2	? 2 3 3	? 50.0 40.0 40.0	42.9
1989	3 5 5 7 4	4.8	2 2 3 4 2	1 3 2 3 2	66.7 40.0 60.0 57.1 50.0	54.2
1990	5 8 5 6 4	5.6	? 4 2 3 2	? 4 3 3 2	? 50.0 40.0 50.0 50.0	47.8
1991	6 9 3 5	5.8	3 4 2 2	3 5 1 3	50.0 44.4 66.7 40.0	47.8
1992	7 7 2 4	5.0	3 ? 2 2	4 ? 0 2	42.9 ? 100 50.0	53.9
1993	7 7 8 9 9 5	7.5	4 ? 4 6 6 3	3 ? 4 3 3 2	57.1 ? 50.0 66.7 66.7 60.0	60.5

Table 5.4 continued

Year	Number of pups	Average number of pups	Number of female pups in each litter	Number of male pups in each litter	% of females among pups in each litter	% of females among all pups investigated
1994	7	7.1	?	?	?	61.1
	7		?	?	?	
	6		4	2	66.7	
	9		5	4	55.6	
	8		4	4	50.0	
	9		6	3	66.7	
	4		3	1	75.0	
1995	8	4.8	3	5	37.5	48.7
	4		?	?	?	
	7		3	4	42.9	
	3		3	0	100	
	3		1	2	33.3	
	4		2	2	50.0	
	5		3	2	60.0	
	3		1	2	33.3	
	6		3	3	50.0	
1996	8	5.1	4	4	50.0	39.0
	8		3	5	37.5	
	3		2	6	25.0	
	4		0	4	0	
	6		3	3	50.0	
	4		1	3	25.0	
	5		2	3	40.0	
	3		1	2	33.3	
1997	8	5.6	4	4	50.0	53.6
	6		3	3	50.0	
	5		3	2	60.0	
	3		2	1	66.7	
	6		3	3	50.0	
1998	7	7.4	4	3	57.1	67.6
	6		5	1	83.3	
	9		6	3	66.7	
	7		6	1	85.7	
	8		4	4	50.0	
1999	8	7.7	4	4	50.0	69.6
	9		7	2	77.8	
	3		3	0	100	
	10		8	2	80.0	
	9		5	4	55.6	
	7		5	2	71.4	

Table 5.4 continued. Wolf breeding data based on nest findings, Paazerje Forest, northern Belarus, 1985-2003

Year	Number of pups	Average number of pups	Number of female pups in each litter	Number of male pups in each litter	% of females among pups in each litter	% of females among all pups investigated
2000	6 5 9 9 6 7	7.0	3 5 5 7 3 6	3 0 4 2 3 1	50.0 100 55.6 77.8 50.0 85.7	69.0
2001	5 7 6 6	6.0	3 4 3 3	2 3 3 3	60.0 57.1 50.0 50.0	54.2
2002	9 7 7 7 8	7.6)	6 4 3 4 5	3 3 4 3 3	66.7 57.1 42.9 57.1 62.5	57.9
2003	4 6 5 8 6	5.8	2 3 1 4 5	2 3 4 4 1	50.0 50.0 20.0 50.0 83.3	51.7

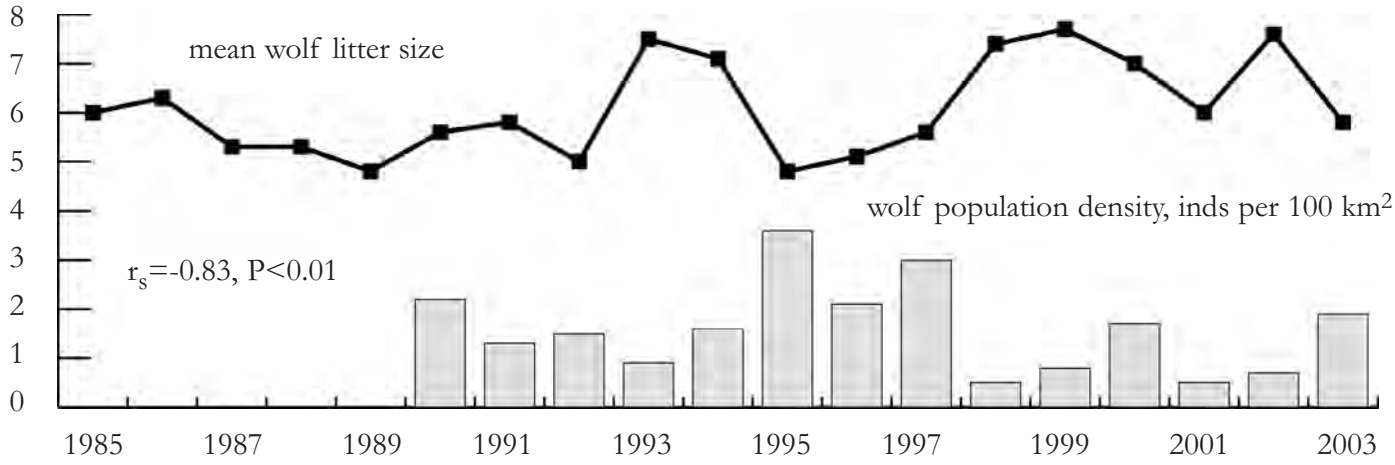
often, when their males are gone for foraging. What is the danger for such a female wolf? It may be a herd of bison or a pack of big stray dogs, but, first of all, adult lynxes. Particularly big male lynxes are a real danger for heavily pregnant female wolves. In our experience, twice we found such a heavily pregnant female wolf, undoubtedly killed by lynxes (Paazierre Forest, 1999; Naliboki Forest, 2012). Moreover, in May 2017 in Naliboki Forest we discovered one more pregnant female wolf that was killed by either wolf or lynx. The head and neck were horribly bitten by one of the species, but which one was hard to identify. We were sure that the pregnant female was not shot. So, not all the registered portion of fertile female wolves, actually breed.

5.2. Fecundity and its density-dependent variation

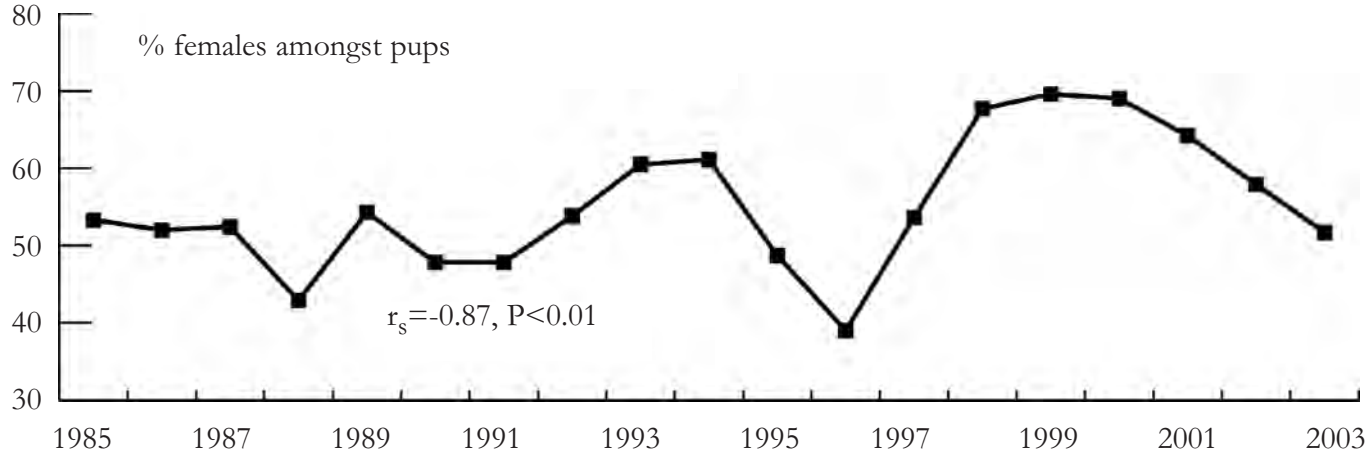
To estimate the fecundity in wolves in Belarus and check the influence of the population density and prey supply on this breeding parameter, we obtained the three following data sets. First, we estimated the number of non-resorbing embryos in pregnant female wolves, which were killed by hunters in different areas in Belarus, where we could get more or less veracious information on the wolf population density and prey supply. So, these fecundity data were plotted against gradients of these two possible factors (see Table 5.2). Second, we gained long-term (1985-2003) raw data of the wolf litter size in relation to the species population density in Paazierre Forest, northern Belarus in the conditions of a relatively poor prey supply (1993-1998) or moderate prey supply (Tables 5.3, 5.4 and 6.1). Third, we gained wolf fecundity data (as size of litter with pups of early days) that originated from Naliboki Forest in the conditions of very rich prey supply, when in 1999-2013 all possible prey of wolves (roe deer, red deer, elks, wild boars and beavers) and wolves themselves were common i.e. rich prey supply as well as when wolf food base was moderate (Table 6.1).

However, before we analyze the above fecundity data, it is important to notice that in Belarus the wolf pregnancy was characterized by fairly high resorption of embryos – on average about 16%. It seems to relate to the species population density: low density of wolves – 8% of resorbing embryos, medium – 20% (G=5.3, P=0.01), high – 18%. Concerning the number of non-resorbing embryos per pregnant female wolf, it varied from 2 to 13, and averaged from 5.0 to 8.9 in different situations in relation to the wolf population density and prey supply (Table 5.2). Looking at these data, we did not notice any fecundity change that could be directed along the gradient of prey supply. At the same time, this fecundity parameter had markedly higher values, when the species population density was low ($U>47$, $P<0.01$).

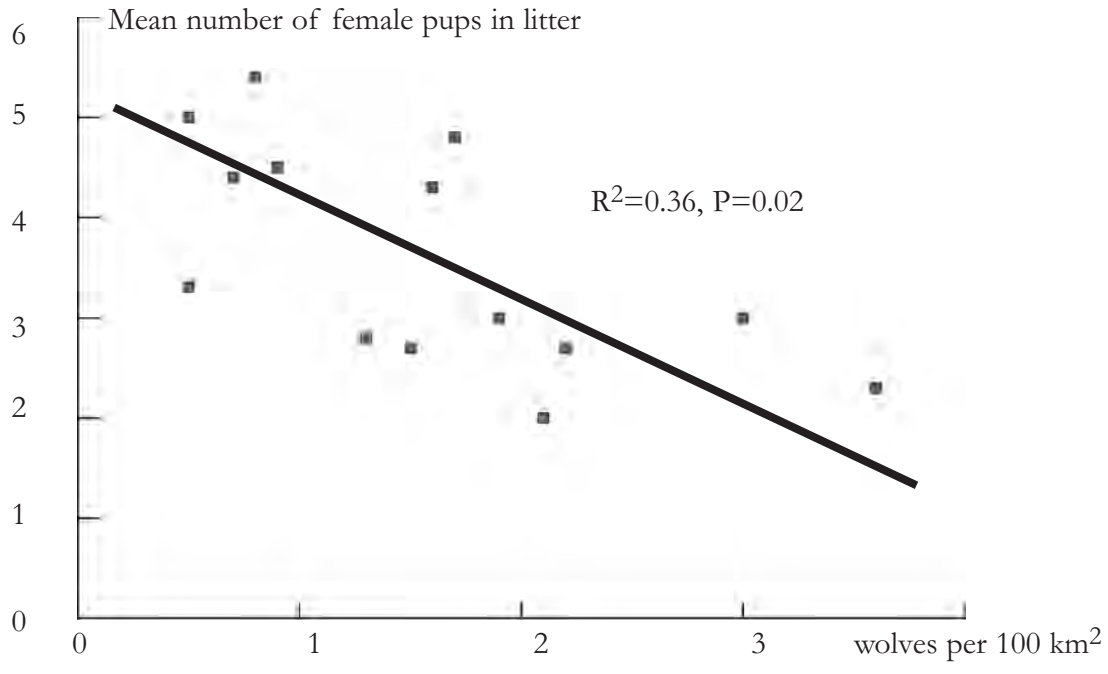
As it was already noticed, we have got detailed data on wolf litter size in relation to the species population density in Paazierre Forest in the conditions of relatively poor prey supply or moderate prey supply (Tables 5.3 and 5.4). While analyzing them, the following results were obtained. The indices of wolf abundance were significantly negatively correlated with the summed harvest in the two preceding years. This suggests that fluctuations in wolf numbers between 1990 and 2003 in Paazierre Forest were considerably affected through persecution by humans ($R^2=0.36$, $P=0.025$ for wolf trail counting;



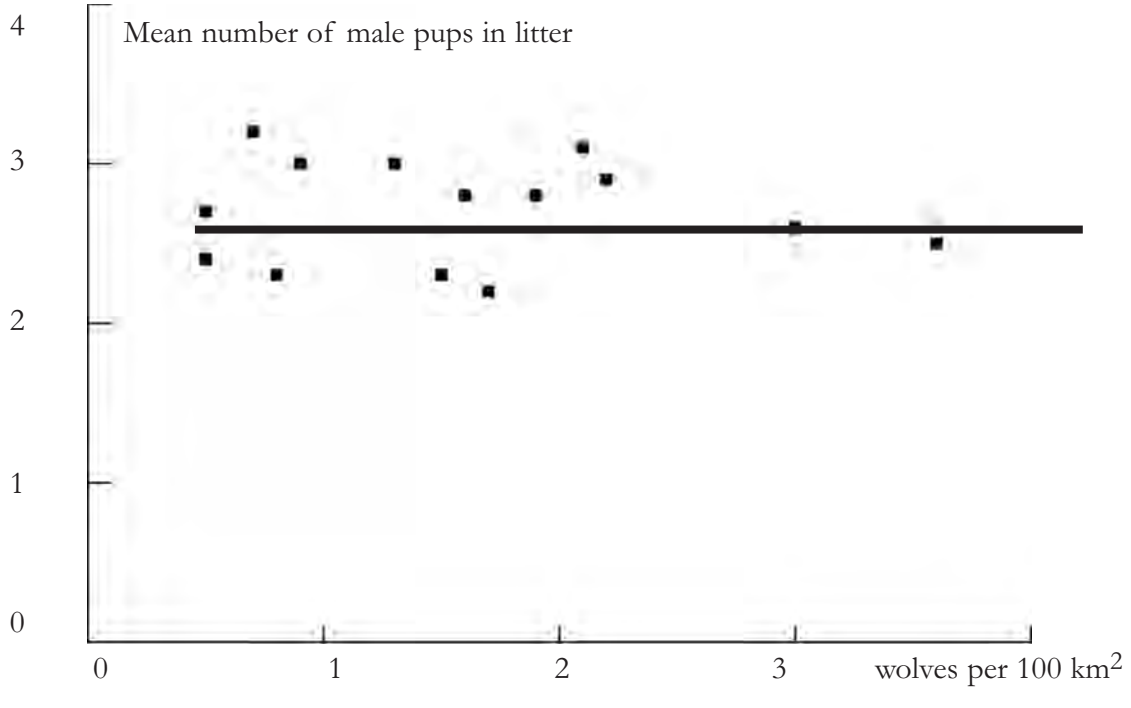
Graph 5.1. Between-year changes in the wolf litter size in relation to the species population density in Paazierre Forest, the northern part of Belarus, 1985-2003



Graph 5.2. Between-year changes in the portion of females amongst wolf pups in relation to the species population density in Paazierre Forest, the northern part of Belarus, 1985-2003



Graph 5.3. Density-dependent changes in the portion of females amongst wolf pups in Paazierre Forest, the northern part of Belarus, 1985-2003



Graph 5.4. Density-dependent changes in the portion of males amongst wolf pups in Paazierre Forest, the northern part of Belarus, 1985-2003

R^2=0.30, P=0.04 for wolf density estimated by local game husbandries, n=14 years; data in Table 5.3).

Connecting litter size and percentage of females among pups with population density, the following statistically significant regressions were found:

(1) mean litter size related to population density – Y=7.55-0.79X, R^2=0.49, P=0.006;

(2) mean number of female pups in litter related to population density – Y=3.35-0.49X, R^2=0.36, P=0.02;

(3) mean litter size related to wolf trail counting – Y=7.27-0.88X, R^2=0.48, P=0.006;

(4) mean number of female pups in litter related to wolf trail counting – Y=2.98-0.52X, R^2=0.52, P=0.004;

(5) percentage of females among pups related to population density –Y=63.3-4.9X, R^2=0.30, P=0.05;

(6) percentage of females among pups related to wolf trail counting –Y=61.1-8.3X, R^2=0.57, P=0.002.

In Paazierre Forest the litter size of wolves varied from 2 to 10 pups, averaging 6.1 (Table 5.4); the pups were up to 20 days old only. There was a clear between-year variation in the mean litter size from 4.8 to 7.7 pups. Litter size was significantly negatively related to the indices of population density. The inversely density-dependent increase in litter size concerned only female pups (Graphs 5.1-5.4). The average number of females in a litter varied from 2 at the highest population density to 5.4 at the lowest population density. The number of male pups in a litter was not related to wolf population density and averaged 2.8 pups for all litters between 1990 and 2003. A similar trend was revealed in relation to the sex-ratio in wolf pups. The lower the wolf density, the bigger proportion of females amongst pups was recorded (Table 5.4). Similar results were found in the North America (Mech, 1975).

Overall, the sex ratio of pups did not differ significantly from 1:1; 55.5% were females and 44.5% were males (G=1.2, P>0.1). Between-year variations of the proportion of females among pups varied from 39.0 to 69.6%. In the years of fairly low population density in wolves (1998-2003) the proportion of females among pups was higher than the one during the last wolf population peak in 1995-1997: 51.7-69.6 (mean 61.7)% versus 39.0-53.6 (47.1)%. However, the difference in means was not statistically significant (G=2.0, P>0.1). Nevertheless, by comparing the proportion of females among pups during only the first three years of the low wolf population density with that one in the period of the increased

wolf population density, shows that the difference in means was more pronounced and statistically significant: 67.6-69.6 (68.7)% versus 39.0-53.6 (47.1)% (G=4.2, P=0.04).

So, we found pronounced density-dependent regulations in the wolf reproduction in Paazierre Forest. The increased fecundity and prevalence of females amongst pups, potentially provided the population growth. This finding, may suggest how they can persist in conditions of heavy persecution by human.

However, the question remains as to why, with an increase in litter size, the number of female pups increases but the number of males does not. The very early age of pups reported in our study (< one month) suggests that sex-biased maternal investment, perhaps, takes place at the stage of conception or mortality in utero.

Also, we assessed litter size in the local population of wolves in Naliboki Forest in the conditions of a very rich prey supply in 1999-2013 and at the same time the quite changeable wolf population density from 0.9 to 2.5 (mean 1.8) inds per 100 km^2. The limited number of findings (only for 38 litters the number of pups was counted precisely) does not provide the estimation of the litter size for every year. Therefore, we averaged litter size for the whole period. Surprisingly, because this was conducted in the condition of such a huge prey diversity and biomass (see the Chapter 2), the mean wolf litter size was only 5.6 pups; cf. in the conditions of poor or moderate food base for wolves in Paazierre Forest the species litter size averaged 6.1 (the range of between-year means was 4.8-7.7).

With respect to that, it is interesting to mention the following situation that appeared since April 2013. The winter of 2012-2013 was very harsh, especially its end with huge snowfall. In this harsh conditions, most of the roe deer and wild boars died, so, prey supply for wolves in Naliboki Forest declined seriously. Since April 2013 till 2017 in the conditions of the lower supply of wolves with prey in Naliboki Forest, we only got to know the precise number of early days pups for 5 litters; 11, 9, 4, 5, 7 and 6 pups that is 7.0 on average. The average wolf density was slightly lower in the winters of 2013-2017 in Naliboki Forest than before - 1.4 inds per 100 km^2 on average.

The above data suggest not much about the food base-related changes in the wolf fecundity. However, the rather low litter size (only 5.6) in the conditions of a very rich (markedly richer than in all other cases) prey supply once more suggests that prey supply does drive fecundity in wolves in Belarus.

5.3. Pack multi-breeding as a density-dependent reproduction regulation in wolves

Multi-breeding in wolf packs is an already numerically registered phenomenon in the wolf population of both North America (see Mech & Boitani, 2003 and references therein) and Eurasia (Danilov *et al.*, 1985; Sidorovich, 2011, 2016). In the wolf monography by Mech and Boitani (2003) there were two factors raised that could be responsible for such a breeding peculiarity in wolves: rich food base (Mech *et al.*, 1998) and a high rate of wolf extermination by humans (Ballard *et al.*, 1987). Anyway, taking into account all the mentioned suggestions in the monography, it looks like the discussion on multiple breeding in wolf packs by Mech and Boitani (2003) is biased to the hypothesis that a rich prey supply is the express condition for that.

A few years ago, we tended to the same inference (Sidorovich & Rotenko, 2014), when our data on multiple breeding in wolf pack was as follows: 3 cases in the conditions of low density in wolves and poor or moderate prey supply; and 7 cases in the conditions of rich prey supply and medium or high local density in wolves.

Nowadays after the study results of 2014-2019 in Naliboki Forest particularly in the conditions of moderate or even poor prey supply in 2014-2015, the above-mentioned ratio appeared as 12 to 7, respectively: 12 cases in the conditions of low density in wolves and poor or moderate prey supply; and 7 cases in the conditions of rich prey supply and medium or high local density in wolves. So, we got more cases on multiple breeding in the conditions of non-rich prey supply.

Also, if we don't consider the population density of wolves on a local scale but on a bigger scale, covering a larger terrain including the forest massif with a reserve (like Naliboki Forest) and also continuous rural areas and agriculture-forest mosaics, where wolves are heavily persecuted each year, it appears that the whole wolf population in Belarus actually has relatively low population density.

Indeed, each year the extermination of wolves in game areas leads to an 'unsaturated' wolf population even in the post-reproductive period. Moreover, each year before the mating season of wolves starts, about a half of wolves are usually killed by hunters. Thus, in Belarus, while mating, wolves are actually in the conditions of a rarefied population with a lot of vacant habitat carrying capacity. Such conditions may lead to the population reacting on the situation by a breeding intensification.

Coming back to the registered cases of multiple breeding in wolf packs in Belarus, let's

say that the majority of the cases of wolf multiple breeding in Naliboki Forest and Paazierre Forest (17 out of 19) were registered in the conditions of a low density of the whole wolf population. As to food base at breeding, in 12 cases the food base was poor or moderate and in 7 cases the food base was rich.

The above leads us to assume that multiple breeding in wolves, at least in Belarus, originated to increase reproduction in the conditions of a low density and heavily persecuted population. In other words, we have such a density-dependent regulation of wolf reproduction in Belarus.

This phenomenon of multiple breeding in a wolf pack is so interesting and may originate from several different situations, that it is justified that each case should be described. While describing multiple breeding cases, we pay attention to the following details: when and where did the multiple breeding happen; what was known about the wolf breeding group; and how were these individuals distributed during the denning period (usually late April till end of June) and afterwards; how many litters were registered in the pack; were the pups in the litters between-litter mixed or not; what were the local and population-wide densities of wolves; what was the prey supply. We will describe the multiple breeding cases, starting with the most recent one and finishing with the first one discovered by us.

Case 19. 2019; Naliboki Forest; the breeder group consisted of two breeding females of unknown origin and founding male; pups of both litters were born in early May on the distance of about one km. The local wolf density was low and the population-wide density of wolves was low; food base was moderate.

Case 18. 2019; Naliboki Forest; two breeding females of unknown origin and founding male; pups from the first litter were born in the mid April and the second one in early May; the denning plots were on the distance of about 3 km. The male served regularly for both mothers. In the second half of May both mothers with their pups were nearby to each other. One litter was disappeared in the late May (there is much support that the pups were killed by lynx), and this unlucky mother started assisting another mother with the litter of 5 pups. The local wolf density was low and the population-wide density of wolves was low; food base was moderate.

Case 17. 2018; Naliboki Forest; two breeding females of unknown origin and founding male; both litters appeared in late May, and the distance between early dens of the two mothers were plausibly within the same plot of one km^2. The

(211←) *On 11th May 2013 in the central part of Naliboki Forest there were found three wolf litters aged as about a month old, two weeks old and few days old. The dens were situated on the distance of about 220 meters, 430 meters and 380 meters. Evidently, we faced with a multiple breeding phenomenon in the wolf pack, whereas the mothers were closely related, perhaps, they were the last year mother and her two daughters. The two elder litters were mixed due to the mother's confusion or stealing of the pups from each other.*

(212↓) *Wolf amateurs John Griffiths (at the right) and Keith Millar (at the left) keep the pups from one of the mixed litters (the case 9 of multiple breeding in a wolf pack. Two pups of 15-18 days old are in Keith's hands and two pups of about 40 days old are in John's hands. Naliboki Forest, 11th of May of 2013.*

male served regularly for both mothers and there were subordinated two non-relative pup-sitters. In July and August there were 10 pups of the two litters, which stayed altogether with the pup-sitters in homesite of about 10 hectars. Parents regularly (every day several times) fed them. Six pups disappeared in the first half of September. Perhaps they were killed by lynx, when hunters disturbed the family heavily. The local wolf density was low and the population-wide density of wolves was low; food base was moderate.

Case 16. 2018; Naliboki Forest; two breeding females of unknown origin and founding male; both litters appeared in late April, and the distance between early dens of the two mothers was 2-4 km. The male served regularly for both mothers. One litter was dissapeared in the late May (there is much support that the pups were killed by lynx), three survived pups of another litter suddenly disappeared in the late September. The local wolf density was low and the population-wide density of wolves was low; food base was moderate.

Case 15. 2017; Naliboki Forest; two different wolf pairs of related wolves, which originated from the winter pack of 7 wolves; the first litter was born in late April and the second one in early May on the distance of about 5 km apart, then in early June both litters were moved within the same treefall area of about one km in diameter and stayed there for a month, at least. The local wolf density was medium, but the population-wide density of wolves was low; food base was moderate.

Case 14. May-June 2017; Naliboki Forest; five adult wolves stayed together the whole winter, the pack consisted of three females and two males, both males were rather big; quite often one of the male walked separately from the group; all three females appeared to be pregnant and in the second half of April they gave birth on the distance of 0.92, 0.72 and 0.95 km from each other; one male mostly looked after two breeding females, whereas the other male took care about the third breeding female; in one of the dens all these wolves were registered altogether on 1st May; two litters were killed by a male lynx in the end of April and the first days of May, whereas the third litter disappeared till mid-June; afterwards the five wolves started walking widely within the previous winter home range and were marking a lot; the local and population-wide wolf density was low; food base was moderate.

Case 13. 2016; Naliboki Forest; an adult male with an unusually small daughter of 3 years old and a quite old female (mother of the daughter; its age was at least 6, but more plausible even 8 years old); these three wolves were the only composition of

the pack during the whole winter 2015-2016; both females got pregnant and stayed together till May, but just a few days before the mother parturition in early May 2016 the daughter separated; it denned on the distance of 2-4 km from the mothers' den a week later; the male looked after both of the females; during June and July the pups of both litters disappeared gradually; in August-September both mothers had disappeared and only the male was frequently registered in the denning areas of both females; a fairly big male lynx was often registered in the wolf denning areas sometimes a few minutes after the wolves; we guess that the lynx killed the pups and possibly both mothers; the local wolf density was medium, but the population-wide density of wolves was low; food base was moderate.

Case 12. 2016; Naliboki Forest; almost the same situation as in case 15; this pack also originated from the winter pack of 7 (and in the late winter only 6) wolves on the same territory; in February 2016 a big female from the pack (may be the founding one) was killed; in the spring 2016 there were two breeding females; one of them denned in mid-April and another in mid-May on the distance of about 3-5 km; then in early June they stayed on the distance of 0.5-2 km away from each other; perhaps both mothers were tended by the same male; in mid-June one of the litters was

(213) *Howling for wolves in August-September is very useful to precise multiple breeding in wolf packs.*

(214) *Wolf founding male is answering to my provoking howling.*

trampled by a bison herd; in the other litter the majority of the pups survived till winter; local wolf density was medium, but the population-wide density of wolves was low; food base was moderate.

Case 11. 2015; Naliboki Forest; almost the same story as number 13; the same adult male with the same unusually small daughter of 2 years old and this quite old female (mother of the daughter), were again the only composition of the pack during the whole winter of 2014-2015; both females got pregnant and stayed together all the time and gave birth within the area of one km^2; when we discovered the dens, they were on the distance of 0.4 km only; the pups were not between-litter mixed; both litters did not survive until winter; local wolf density was medium, but the population-wide density of wolves was low; food base was poor.

Case 10. 2014; Naliboki Forest; during May, in one wolf denning area we failed to discover the wolf den with the pups, and at the same time, while searching for wolf pups, a lot of features suggested that there were two litters in that area; later in September-October by howling for wolves there, simultaneously we got answers from two litters with adults on a quite short distance between them - about 0.5-1 km; in early September local foresters saw a wolf family group with five adult (relatively big) wolves and many pups (about 10) with a markedly different size; the wolf group was crossing the road about 30 meters in front of the vehicle, and foresters saw them very clear; during the winter 2014-2015 there were two large wolf packs in the area having 7 and 9 individuals; the pack home ranges overlapped considerably; the local population density in wolves was high, but the population-wide wolf density was low; food base was poor.

Case 9. 2013; Naliboki Forest; on the 11th of May three wolf litters were find in close proximity; the distance between the actual dens were 0.38, 0.22 and 0.43 km; one litter was about 40 days old, the second about 15-18 days old, the third consisted of small blind pups; the first and second litters were mixed as 2 and 2 in one and as 2 and 5 in the other one; in late May four adult wolves walked together in the denning area, so, there was only one adult male tending them; the 'three-mother family' stayed together till mid-July, then they started separating; not one pup of the three litters survived till the next winter of 2013-1014; the four breeders originated from the pack of 10 wolves of the previous winter of 2012-2013, and the next winter of 2013-2014 there were only 9 adults and subadults; the local population density in wolves was rather high, and the

population-wide wolf density was medium; food base was rich till late April 2013, then rather poor due to the collapse in the populations of the roe deer and wild boar.

Case 8. 2013; Naliboki Forest; there were two breeding females with their denning sites on the distance of 2-3 km; perhaps the same adult male looked after both mothers; the breeders originated from the pack of 4-6 wolves during the previous winter of 2012-2013; in mid-January 2013 a big female from the pack (perhaps, founding one) was killed; the two mothers separated in August 2013 and one of the mothers with pups moved towards an agriculture-forest mosaic quite faraway (5-7 km) from the denning area; the rest of their story is unknown; the other mother with 4 survived pups created a pack of seven individuals and stayed in the same territory as the one during the previous winter; the local population density in wolves was rather high, and the population-wide wolf density was medium; food base was rich till late April 2013, then rather poor due to the collapse in the populations of the roe deer and wild boar.

Case 7. 2012; Naliboki Forest; in late April we detected a wolf breeding pair with a litter of about 10 days old; we failed to see the pups, but their presence in the place was very evident; on 21st May on the distance of 2.2 km from the mentioned denning site we discovered another wolf den with 11 pups, which were still mostly blind, *i.e.* about 8-10 days old; it looked like the same big male wolf tended the two mothers; until the mid-October all these wolves stayed in that area of about 20 km^2; in September the two litters answered easily on our numerous howling from the same fixed point, the answers were coming from different directions on the distance of 1-2 km apart ; in the late November till mid-January all these wolves lived in a pack of 16 individuals; in the late January this large pack split up in two packs of 6 and 10 individuals; local wolf density was medium, and the population-wide density of wolves was low; food base was rich.

Case 6. 2010; Naliboki Forest; half of a pack was exterminated during winter of 2009-2010; but the founding male and female and their daughter on the second year of life survived; both females gave birth in May; the daughters' pups were about 20 days younger; the distance between the mothers' den sites was 3.8 km, when we found them in the end of May; in June, while hunting, the male walked together with both breeding females; altogether six pups survived till December 2010; the big male (father), two mothers and the six pups created a pack for the whole winter 2010-2011; in March of 2011 the pack was extirpated by

hunters; local wolf density was high, but the population-wide density of wolves was medium; food base was rich.

Case 5. 2010; Naliboki Forest; in the beginning of May we discovered a wolf denning site with 37 dens, which were recently used a lot; there was evidence that pups were born not later than 20th of April; we did not find those pups, because we discovered the denning site in the evening and we were pressed for time to find all the dens; at night the pups were relocated by the parents not far away, but we did not disturb them anymore; on the 21th of May on the distance of 2.7 km from the above-mentioned denning site we found an early den of another female wolf with small blind pups; it looked like to different males (with a clear difference in the footprints' sizes) took care about the mothers and their litters; the families live lived there approximately till October, when one of the family left the area; local wolf density was high, but the population-wide density of wolves was medium; food base was rich.

Case 4. 2004; Naliboki Forest; on the 17th and 19th of May we found two different wolf litters of the pack-founding female and another mother; the distance between the den site locations was 1.6 km; another mother was often visited by a son (marked with finger clipping) of the founding female; the son was three years old; in June-July all the wolves with the two litters stayed together, then the mothers began to keep some distance between their locations; in September the two litters answered on our howling still from one point; then in late November it was learned with snowtracking that the founding pair stayed with 4 pups and 2 more rather big wolves, while the other mother with the son of the founding female and 2 pups separated from the founding pair and settled on the distance 4-9 km away, in December they were killed; local wolf density was medium, but the population-wide density of wolves was low; food base was rich.

Case 3. 2003; Paazierre Forest; during the last days of January, the majority of individuals a big pack of wolves including the founding female were extirpated; a big male and two other markedly smaller individuals survived; one of the individuals was the daughter of the founding female of 2 years old (marked with clipped finger); there were two wolf litters with mixed differently aged pups on the distance of about 0.8 km; the local population density in wolves was medium, but the population-wide wolf density was low; food base was moderate.

Case 2. May-June 2000; Paazierre Forest; on the 7th of May in an abandoned peatory, which was densely inhabited by beavers

(215-218) *On the above photo you see female stray dog, which naturalized in the habitats of Naliboki Forest and paired with a male wolf. The female dog stayed with the male wolf, at least, four months (mid January-mid April, 2016) in the late April it gave birth in the wild and then brought the pups to the former owner yard (see the upper right photos); one of the hybrid pup was such a white one.*

and wild boars, we discovered two litters on the distance of about 2 km; one litter with pups of 15-20 days old belonged to the founding female, whereas the other one with blind pups originated from its daughter (marked with clipped finger); in the mid-June and the end of August the litters and their mothers were registered staying in the same places; also two marked males on the third year of life (the mothers' sons) and a big male (perhaps the father) were registered at the litters; the rest of this family story was not followed, but in December 2000 in the pack area there were 10 wolves killed that plausibly were from the double-breeding pack; the local population density in wolves was medium, but the population-wide wolf density was low; locally the food base was rich.

Case 1. 1999; Paazierre Forest; 4 individuals were killed from the wolf pack of 8 wolves in the end of January; among the killed wolves there was big (perhaps, founding) female; in February two survived daughters on the second year of life (marked with clipped finger) copulated with their father, while the fourth individual dispersed; the daughters gave birth in the sites placed about 3 km apart; the rest of this family story was not followed; the local population density in wolves was medium, but the population-wide wolf density was low; food base was moderate.

Also, we would like to say that during our long-term experience with wolf denning and getting a lot of messages from wolf-related people (wolf amateurs, hunters, foresters *etc.*), we heard of many more cases of seemingly multiple breeding in a wolf pack. However, we considered in this book only those our own cases, for which we have got enough and reliable information on.

Next to the above-described 19 findings of multiple breeding in wolf packs in Naliboki Forest and Paazierre Forest, we also gained evidences on the investigated wolf carcasses. To be sure about this information, the whole pack that was killed in March or April should be only controlled.

During our long period of wolf study, we investigated only nine such wolf packs that were killed in March or April. They consisted of 3 to 10 wolves. Each pack had, at least, one breeding female. In one case two females were pregnant. In another case in a pack of 9 wolves there were four females; three of them were pregnant and one was still in estrus or in a very early pregnancy. In all these cases, the population-wide density was low and food supply was mostly poor or moderate. Only in the cases of one pack with one pregnant female and the case of the pack with two pregnant females the food base may be defined as rich.

(219-224) *On these photos you see the members of one wolf pack that consisted of 7 individuals. The outstanding feature of this pack was that the mother is a wolf-stray dog hybrid (see it on the upper right photo).*

(225, 226) *Domestic dog that was killed by wolves on the owner yard.*

(227) *Owner is showing the chain leash, from which his dog was tired out by wolves.*

Thus, the above presented material makes sure that in Belarus the phenomenon of multiple breeding in a wolf pack is common. It is evidently connected with the low density of the whole wolf population, and looks like irrespective of food base. We consider multiple breeding in wolf packs as a population reaction on the unsaturated state and relatively low density, and this response is directed to increase the reproduction and compensate the loss from persecution mainly by humans.

However, another important question arises: how often does multiple breeding in wolf packs occur? The findings of multiple breeding in wolf packs should be related not to the number of wolf dens with pups, which were discovered by us (n=74), but to the numbers of wolf denning cases, which were investigated and for which the phenomenon was more or less sufficiently controlled. Searching for wolf dens and while investigating denning of wolves with camera-traps as well as by means of registration

(228, 229↑↓) *These hybrid pups had a white spot on their breasts that is rare feature in normal wolf pups in Belarus.*

(230↑) *This is a rare occasion of winter breeding of wolf-dog couple. The mother was a big dog and the father was a normal fairly big wolf. Denning behavior of the breeding pair was entirely typical for normal wolf couple in May, i.e. denning at a root plate of uprooted spruce, which is situated among tree windfall. The den area was located in a remote forest fragment on the distance of 2.1 km from the nearest hamlet and about 300 meters from the nearest terrain road. All these typical behavioral features of breeding female wolf suggest that the dog mother may be already a wolf-dog hybrid and it was already raised in the wild by parents, one of which was a wolf. In this case of wolf-dog hybridization the wolf population density was low, and the food base was rich.*

(231, 232↓) *One of this hybrid pup of 7 months old. It was abnormally big one compared a wolf pup of this age - about 50 kg. The hybrid muzzle, canines and other teeth were like in wolves. Other two pups, which were raised by people, were smaller and had dog' features.*

of pup presence by their tracks, a total we learnt more or less sufficiently about denning in 59 wolf breeding groups. During this study we revealed 17 cases of double breeding and 2 cases of triple breeding in a wolf pack (actually in a wolf breeding group *i.e.* a couple or larger breeding group up to five adult wolves). So, at least, in 32% of the investigated denning cases there was registered a multiple breeding phenomenon in wolf packs. The main reason for multiple breeding was mating of the dominant (founding) male not only with the founding female (mother), but with daughters or other subdominant females. Taking into account that not in all cases the possibility of multiple breeding was checked sufficiently detailed, *i.e.* when other possible litters could be not discovered, we assume that actually multiple breeding in wolf packs occurs even more often than can be derived from our data.

Concerning the wolf carcass material, the frequency of multi-breeding is about 22% of the investigated cases (n=9).

5.4. Hybridization with stray dogs as a response of overexploited wolf population to compensate the loss

Hybridization of wolves and domestic (actually stray) dogs is a question worthwhile to consider in the aspect of the wolf reproduction biology. Firstly, it relates to breeding of wolves; secondly, such a hybridization may be considered as the extreme effort of the last wolf individuals to maintain the declined population with such an abnormal reproduction.

Some deliberate hybridization between a wolf and a hunting dog was known in Belarus from the Middle Ages (at the time the Great Lithuania). For instance, this was mentioned, for several times in the Radzivils' metrics for the magnate game economy. Not once they mentioned that such a hybridization was revealed somehow in the wild. However, still sometimes people (mainly game-related) try to produce wolf-dog hybrids in Belarus without a strong reason for that. As to such hybridization in the wild terrain, a few cases of wolf and domestic dog interbreeding were known in the 1980s, 1990s and early 2000s in different districts in Belarus. We assume that it used to happen, but only quite rare. Therefore, when we sampled wolves in Belarus in the early 2000s for a genetic study, none of these wolves showed dog ancestry (Stronen et al., 2013).

Since 2010, cases of wolf-dog hybridization were registered markedly more often. Personally, we registered seven such cases, for which we saw a lot of details or we found the dens ourselves. For four cases the prey supply was rich or very rich, and the wolf population density was low. In one case the prey supply was rich, and the wolf population density was medium locally, but population-wide it was low. In two cases the prey supply was moderate, and the wolf population density was medium locally, but population-wide it was low.

From the above material, which is not very extended, but anyway, it looks like that in Belarus mostly two possible factors determine wolf-dog hybridization: rich prey supply and low density of the wolf population. Nevertheless, wolf and domestic dog interbreeding may happen in another situation, when the wolf population density is not so low, and it is possible for a sexually matured wolf to find a mate. Also, food base may be not so rich. Two cases in Naliboki Forest (June 2014 and April 2016), which were investigated by us in detail, suggest the above statements.

As to the denning behavior of such a wolf-dog pair, we gained quite interesting information that was already given in Chapter 4.

A very interesting question, is how such a wolf-dog pair is created, because in Belarus it is so common that wolves kill domestic dogs as much as possible even on a peasants' yard and in mating season (*e.g.* Sidorovich, 2011). We will say that the killing of domestic dogs by wolves mostly happened during January-March, *i.e.* the mating season in wolves, and before and after mating. Fairly often wolves eat such victim-dogs. Interestingly, what induces the behavioral switch of wolves from such an aggression towards dogs to a courtship and copulation with them.

Concerning that we propose the following hypothesis. An adult male wolf may pair with an adult female dog, which lives as a wolf in a wild terrain by providing food for itself (hunting and or scavenging) and it keeps a territory with intensive making. So, indeed such a stray dog lives like a wolf. In the ambient conditions of Belarus with a harsh winter this is only feasible for a smart dog , if there are many preys and carrion from the dead prey. Therefore, the factor of a rich prey supply is so important. Such a stray dog naturalizes in dog pairs quite often. In such a case, the male wolf kills the male dog and pairs up with the female dog.

Indeed, among the seven studied cases mentioned above, there were four cases, in which it was known that the female dogs stayed in the wild terrain for long (longer than half a year). In two of these four cases the female dogs stayed with a male

dog, and those male dogs disappeared after pairing of the female dog with a male wolf. In all seven cases only female dogs paired with male wolves, but we did not reveal any opposite case, where a male dog paired with a female wolf.

As to captive hybridization of dogs and wolves in Belarus, both ways are used to get hybrids, *i.e.* male wolf-female dog and female wolf-male dog.

The last curious question is why the wolf-dog hybridization was so amplified since 2010. We may only make a comment on this. In Belarus in the beginning of the 2010s, there appeared many commercial game husbandries that breed a lot of wild ungulates with feeding stations and fields. These wild ungulates include not only native, but even exotic species like a mouflon or fallow deer. These non-native ungulate species are not good survivors during quite harsh winters, which commonly happen in Belarus. So, carrion from ungulate carcasses appeared more common in the territory of game husbandries. Moreover, these commercial husbandries are well equipped, have enough finance and wardens to eliminate wolves, sometimes, for several times per year. Moreover, it is usual that hunters avoid killing of stray dogs, because they may belong to another hunter or local peasants. They avoid problems that may appear, if they kill such a dog. So, in such commercial game husbandries there are all the suitable conditions for stray dog naturalizations, their survival may last long enough, and there are a few wolves hardly searching for a mate.

Chapter 6. Mortality in wolf pups with implication for the species population structure

The main monograph on the grey wolf by Mech and Boitani (2003), which still provides the basic and unequalled knowledge on the species biology, informed the following. "Almost 30 years ago, Keith (1974) concluded that "the factors which provide wolf pup mortality during the first 5 months are almost wholly unknown. This is probably the single greatest enigma in wolf biology today. Though some strides have been made toward identifying these factors, this is still a much needed area of research."

While reading this in 2004, we already were much aimed by the question. Moreover, the opportunity to find out something really new in the wolf biology accelerated these our research efforts. Nowadays, we may say that, at least, for the region of Belarus mortality in wolf pups is known more or less. Also, we assume that the factors, which impact the survival of wolf pups in Belarus, act in other regions of European forest zone. At the same time, we suppose that the only main causes of wolf pup mortality were found out, whereas many smaller questions remain unresolved.

This begs the question of how a such complicated research (*i.e.* what factors are likely to influence pup mortality) was posed. In fact, during searching for wolf dens with early day pups and older pups, being in wolf family habitats year-round and for many years, we faced many times with situations of dying or dead pups. The data collected finally clarified the hidden question of wolf pup mortality in Belarus. Also, in 2014-2019 applying of many camera-traps (up to 70) that were well-set helped a lot.

6.1. Mortality causes and estimates of mortality rate in wolf pups

While analyzing mortality and survival in wolf pups, it is worthwhile to begin with the analysis of the influence of environmental factors in connection with complexity of wolf denning behavior. The data of Table 4.1 suggests that burrowing by parents leads the higher survival in pups until the coming winter (r_s=0.40, P=0.03). Long distance replacing of pups leads the lower survival in pups (r_s=-0.41, P=0.02). During rainy weather more complicated denning behavior of wolves (more denning sites, more dens each site and longer distance of replacing between the denning sites) leads the lower pup survival rate (statistically significant with total number of dens only r_s=-0.55, P=0.05). Conversely, during more or less dry weather more complicated wolf

Table 6.1. Survival in wolf pups in each litter traced from the birth (mid-April-May) until autumn (late Spetember-November) in Naliboki Forest (* - 1999-2011, ** - 2012-2015, *** -2016-2017) and Paazierre Forest (1990-2004)

Study area	Number of pups		Survival in pups, %
	May	November	
Naliboki Forest*	7	6	86
Naliboki Forest*	6	0	0
Naliboki Forest*	7	5	71
Naliboki Forest*	5	5	100
Naliboki Forest*	7	6	86
Naliboki Forest*	9	6	67
Naliboki Forest*	8	5	63
Naliboki Forest*	5	4	80
Naliboki Forest*	9	4	44
Naliboki Forest*	6	4	67
Paazierre Forest	5	5	100
Paazierre Forest	6	2	33
Paazierre Forest	9	4	44
Paazierre Forest	8	3	38
Paazierre Forest	6	2	33
Paazierre Forest	9	5	56
Paazierre Forest	10	4	40
Paazierre Forest	9	0	0
Paazierre Forest	7	5	71
Paazierre Forest	8	4	50
Paazierre Forest	3	0	0
Paazierre Forest	4	3	75
Paazierre Forest	5	3	60
Paazierre Forest	7	0	0
Paazierre Forest	9	3	33
Paazierre Forest	6	2	33
Paazierre Forest	2	2	100
Paazierre Forest	6	3	50
Paazierre Forest	5	4	80
Paazierre Forest	7	2	29
Paazierre Forest	8	1	13
Paazierre Forest	9	7	78
Paazierre Forest	5	0	0
Paazierre Forest	9	0	0
Paazierre Forest	9	0	0

Study area	Number of pups		Survival in pups, %
	May	November	
Paazierre Forest	4	3	75
Paazierre Forest	5	4	80
Paazierre Forest	7	5	71
Paazierre Forest	3	3	100
Paazierre Forest	6	4	67
Paazierre Forest	6	5	83
Naliboki Forest***	4	0	0
Naliboki Forest**	11	2	18
Naliboki Forest**	1	1	100
Naliboki Forest***	?	0	0
Naliboki Forest***	?	0	0
Naliboki Forest***	?	0	0
Naliboki Forest***	?	0	0
Naliboki Forest***	?	0	0
Paazierre Forest	5	4	80
Paazierre Forest	8	0	0
Naliboki Forest**	5	1	20
Naliboki Forest **	5	3	60
Naliboki Forest*	9	3	33
Naliboki Forest**	6	5	83
Naliboki Forest*	4	4	100
Naliboki Forest**	7	3	43
Naliboki Forest**	10	3	30
Naliboki Forest*	4	4	100
Naliboki Forest**	5	0	0
Naliboki Forest**	8	0	0
Naliboki Forest**	7	1	14
Naliboki Forest*	6	5	83
Naliboki Forest***	9	0	0
Naliboki Forest***	5-7?	1	17
Naliboki Forest***	6-8?	1	14

denning behavior leads the higher survival rate in pups: correlation with number of denning sites in a given wolf breeders r_s=0.56, P=0.05; with number of burrow in a given wolf breeders r_s=0.54, P=0.05; and with distance of pup replacing between the denning sites r_s=0.57, P=0.04. Number of mosquitos, rainy weather and human presence drive the complexity of denning behavior and may increase the mortality in wolf pups indirectly: rain – total number of wolf dens in a given wolf breeders (r_s=0.38, P=0.04); mosquitos – total number of wolf dens in a given wolf breeders (r_s=0.42, P=0.02); human presence – total number of wolf dens in a given wolf breeders (r_s=0.52, P=0.004); human presence – number of denning sites in a given wolf breeders (r_s=0.68, P=0.00004); human presence – distance between the denning sites on average (r_s=0.46, P=0.01). So in effect all of these, there were found significant correlations: rain – mortality in pups (r_s=0.71, P=0.0002); mosquitos – mortality in pups (r_s=0.51, P=0.04); human presence – mortality in pups (r_s=0.37, P=0.047).

(233) *Wolf pup of 6-8 days old, which was killed and trampled by bigger pups of a month old. These several bigger pups were stolen by mother from another litter in the case of multiple breeding in the wolf pack.*

The above correlations suggest the essential relationships between ambient conditions, complexity of wolf denning behavior and mortality in pups. However, first of all, it is important to get know how and from which kinds of impact wolf pups die. Therefore, by describing and estimating mortality in wolf pups, first of all, we would like to list the revealed cases of pup deaths and respectively which factors were responsible for that.

First, it is a deliberate leaving by wolf parents of some pups to die , while replacing the litter from one den to another one. During our long-term experience of wolf pup searching we discovered on the recent former den one abandoned pup for 5 times, two pups – twice, and once there were four definitely abandoned pups. Mostly the abandoned pups were dead. Normally such a deliberate leaving of a few pups to die happened with a large litter consisted of more than 7 pups (in our materials it was in 5 out of 6 cases, in 2 cases the number of pups was unknown).

The above-mentioned cases of pup abandonment relate to early days pups. However, even older pups of several months old may be abandoned by parents. In the mid and late summer of 2013 in Naliboki Forest in the conditions of the rapidly declined supply with prey we faced with that, at least, for several times (see Chapter 4 for the details).

There is another way, an indirect one, how breeding wolves condition to small pup death. In case of multiple breeding in wolf packs mothers steal pups from each other quite often. They steal not all pups; usually only 1-3 pups are taken from another litter. Actually, in our research experience and in the practice of three other wolf pup searchers (altogether about 160 wolf litters that were looked through) such a denning behavior of stealing pups was registered for 6 times. In the respective litters there were pups of different ages. These mixed litters consisted of 3 and 4 pups of distinctive ages; 4 and 1; 5 and 1; 3 and 2; 7 and 1; 5 and 4. In such a case wolf litter consists of bigger and smaller pups. Sometimes, this size difference may be too much, and bigger pups suppress smaller ones. Such a suppressed small pup die somehow, finally being trampled in the den bedding materials. Twice we faced with such a case of a dead pup or several dead pups in the mixed litters: in one case there were found 2 small pups alive, one small dead pup and 4 markedly bigger pups; in another such a case - 3 small pups alive, 2 small dead pups and 4 markedly bigger pups.

We registered that the wolf pup mortality was significantly higher in larger litter (see Table 6.1). Using these data, we found strong negative correlation between the litter size in May (*i.e.* recently after the birth) and the pup survival until the beginning of the first their winter (r_s=-0.73, P<0.01). Usually, it is like that. If there are 9-12 pups in the mid-May, it means there will be 2 to 4 of them in July; whereas in litters that initially consisted of 1 to 4 pups almost all of them may survive till the first winter. Generally, we suppose that such a dying of wolf pups through a fault of their parents comprise 10-20% of overall pup mortality till the first winter.

Second factor of wolf pup mortality is predation lynxes, particularly by adult male lynxes. Indeed, we found that adult lynxes kill wolf pups quite regularly. As to this impact, we actually registered the following. In Naliboki Forest, 4 wolf litters up to 2 months old were definitely killed by lynxes and killing of 4 other wolf litters up to 2 months old by lynxes was found very plausible. Also, we discovered 8 wolf pups of 2-11 months old, which were killed by lynxes. Mostly adult male lynxes deliberately hunt on wolf pups. While roughly estimating, we

(234-240↑←→) *On these two pages we demonstrate one of the well traced and documented example of lynx interference towards wolves that was directed on the wolf reproduction. In Naliboki Forest in the late April of 2017 in wolf pack consisting of three pregnant females and two adult males (a case of multiple breeding in a pack) appeared three litters. During two weeks all three litters were extirpated by one big male lynx (that you see on the photos). You see appearance of the male lynx at the wolf burrows with pups (there was snowfall on 10th and 11th of May 2017). In one case (photos at the right) there was mother wolf at the den, but, when it detected the lynx, it has escaped, permitting for the lynx to kill the pups.*

29.43 inHg
7℃
05/06/2017 12:55AM CAMERA1

29.43 inHg
8℃
05/06/2017 12:56AM CAMERA1

(241) *Wolf pair that has pups looks for another denning site. On the photo the parent wolves are inspecting former badger sett, where they denned the last spring.*

Table 6.2. Age composition and sex ratio of the wolf population based on analysis of skull collection in relation to hunting pressure, Paazierre Forest, northern Belarus, winters of 1995-2003.

Parameters	Moderate hunting pressure	Heavy hunting pressure	G-test, P
Sample size of the skulls investigated	142	187	
Proportion of juveniles, %	33.8	54.6	4.94, 0.04
Proportion of females among juveniles, %	45.8	68.6	4.57, 0.04
Proportion of yearlings, %	21.1	15.5	0.86, >0.1
Proportion of females among yearlings, %	43.3	58.6	2.31, >0.1
Proportion of adults, %	45.1	29.9	3.10, 0.07
Proportion of females among adults, %	53.1	57.1	0.15, >0.1
Mean age of adults, years	5.1	3.2	
Population mean age, years	2.8	1.5	
Maximal age, years	9+	7+	
Ratio of juveniles over adults, fold	0.75	1.82	

suggest that in Belarus 30-50% wolf pups and even more of them are killed by lynxes in the habitats, where the lynx population density is 2 inds per 100 km^2 and higher (may be up to 6).

One well traced and documented example was quite impressive, at least, for us. In Naliboki Forest in the late April of 2017 in wolf pack consisting of 3 pregnant females and 2 adult males (a case of multiple breeding in a wolf pack) there were born three litters. During two weeks all three litters were extirpated by one big male lynx. Applying camera traps, we documented appearance of the male lynx at the wolf burrows with pups (see Photos 234-240). In one case there was the mother wolf at the den, but, when it detected the lynx, it escaped, permitting for the lynx to kill the pups.

Potentially red foxes, badgers, raccoon dogs, golden eagles and white-tailed eagles may kill wolf pups up to two months old, when parents are absent at the den for foraging and other necessary activity. Nevertheless, we have never faced with that. However, one of the two wolf pup searchers, whom we know life-long and

(225, 226↑↓) *Wolf pups that were killed by lynxes in August and September.*

trust, evidenced that he registered wolf pups that were presumably killed by a red fox. Perhaps, therefore breeding wolves try to extirpate all red foxes in their denning sites. Concerning the other four species of medium-sized predators, we have never heard that in Belarus they attacked wolf pups although it is possible. Nevertheless, in the neighboring Latvia it was found that golden eagles kill and consume wolf pups sometimes (Bergmanis *et al.*, 2012).

Third factor of wolf pup mortality is killing of them by wild ungulates. According to our own findings and information that we received from three other wolf pup searchers, this happens not rarely. Twice there were discovered by us the remains of wolf pups, which were killed and even eaten by wild boars and once we found two carcasses of pups, which killed by roe deer. For three times a lot of fresh elk tracks were found nearby wolf dens; it looked like the elks tried to kill small pups with their hooves, while the pups tried to escape within fairly dense wood cover (dry last year and new grass, dead tree materials with uprooted trees, bushes). None of the killed wolf pups was discovered on the places, but, if they were crashed by the elks, perhaps, their carcasses might be taken by the parents afterwards. Twice the same situation was registered in relation to red deer. In one of these cases carcasses of three wolf pups were found. Twice there were registered, where wolf pups about 2 months old were trampled by bison herd. We suppose that in Belarus killing of wolf pups by wild ungulates usually constitutes up to 10% of overall pup mortality till the first winter. However, if wild ungulates are spread widely in the whole habitat variety and their population density is high (15-20

and more inds per one km^2, except of roe deer), up to a quarter of present wolf pups may be killed by wild ungulates till the first winter. For instance, in Naliboki Forest, where in the last years the density of inimical for wolf pups ungulates is outstandingly high, approximately 20-30% of wolf pups are killed by wild ungulates. We think that stags (adult male red deer) and both sexes of adult elks and bison may be mainly responsible for such a death of wolf pups, first of all.

Another possible factor of wolf pup mortality is piroplasmosis disease. When we look through wolf pups, many of them had ticks: pups that were up to one month old - 43%, n=634; pups of 1-5 months old – 100% (n=32). We do not know how often wolf pups may be ill on piroplasmosis disease and die from that. We merely have an indirect argument for that. Our dog of 15 years old spent almost all its life within our study areas in the places with the same abundance of ticks as the local wolves. This our dog was ill on piroplasmosis disease for three times during these 15 years and, perhaps, could die from that each time. So, we assume that this disease may be also a significant factor of wolf pup mortality, but surely it is not so essential as in the cases of killing of wolf pups by lynxes and wild ungulates.

(227) *Brown bear at wolf den, where there were pups recently.*

During our long-term being in the habitats of wolf families we discovered only two wolf pup carcasses (about 4 months old) that died from an unknown cause, may be piroplasmosis disease or may be other problems. Another wolf amateur and game worker reported that once he faced with two dead wolf pups, and the cause of their deaths was hard to determine, just by inspecting them externally. Anyway, it looks like diseases (*e.g.* piroplasmosis, rabies *etc.*) may be responsible for a relatively low portion of wolf pup mortality, at least, in the Paazierre Forest and Naliboki Forest in Belarus during the period of studies since the mid 1990s. Otherwise we or somebody else could find markedly more wolf pup carcasses in the habitats.

Another factor of possible wolf pup mortality is plausible killing of them by brown bears. In the second half of May 2019 in Naliboki Forest we registered of very plausible killing of wolf pups in den by brown bear. Two brown bears (mating couple) frequently followed the wolf couple at denning, they inspected their dens, and finally the wolf litter has disappeared. In May-June of 2018 in Naliboki Forest again we registered similar behaviour of another adult male bear to another wolf breeders. Moreover, in July-September of 2018 in Naliboki Forest we documented regular visiting of homesite of another wolf family by another male bear. The bear marked that place a lot in three points. Interestingly, that in May-July of 2019 the bear was present that place again, but did not mark all the three points, when there was no regular stay of breeding wolves in the place. All these suggest possible heavy interference between bears and wolves at denning and raising pups in homesites, but still it is a little known about the question.

Among other causes of mortality in wolf pups it should be mentioned killing of them by wolf pup searchers as one of the ways of the species population control. In Belarus it constituted of an essential part of wolf pup mortality until the mid-1980s. That time in more or less well-set game areas (a third part of Belarus), at least, a half of wolf litters were discovered and

(228, 229) *Brown bear at wolf den, where there were pups recently.*

(230, 231) *Brown bear at marking in wolf family homesite and wolf founding male of the family is investigating the bear mark just after the marking by the bear.*

(232) *Pups of the family in their homesite, where the bear was marking yesterday.*

killed by wolf pup searchers every spring. Then wolf pup searching sharply declined, mostly because people, who smart in the wild and easily doing with wildlife began disappearing in the countryside. That was evidently connected with village life declining, relocating of countryside locals in towns and cities, while urban residents are evidently not capable for such a job. Afterwards (the 1990s-2010s) approximately one per 30 to 50 wolf litters was killed by people mostly game-related ones. So, this factor of mortality in wolf pups became not really important nowadays in Belarus.

Road kills of wolf pups and any wolves are rare in Belarus still. During the long-term period of study on wolves in the study areas we revealed only two road kills of wolves. One of the killed wolves was a pup of 5 months old. Normally, information about wolf road kills spreads widely, and we get know easily about such a case.

By evaluating the mortality in wolf pups, we revealed that it is really high. While tracing 33 wolf litters in the period from their birth (mostly first half of May) to the beginning of winter in November-December in Paazierre Forest (Table 6.1), the survival in wolf pups was rather low – 0.48 on average (*i.e.* 52% of pups died during the first 6-7 months).

As to mortality of wolf pups in Naliboki Forest, we separated our material for the three periods characterizing by distinctive state and density in the local population of the lynx (Table 6.1): the first, in 1999-2011 there was low number of lynxes, up to 1.11, on average 0.45 inds per 100 km^2 of forest massif, these years were marked in the table with *; ** - the second period in 2012-2016, 1.16-1.84 lynxes per 100 km^2 of forest massif; *** - the third period in 2016-2018, 2.21-4.43 lynxes per 100 km^2 of forest massif. These three periods were checked separately, because of the marked difference in the lynx population density was found and taking into account that lynxes kill many wolf pups. Respectively, we evaluated that in 1999-2011 with the low number of lynxes the

mortality in wolf pups till the first their winter was about 30% (n=14 litters traced); in 2012-2016 with markedly more lynxes – 63% of wolf pups died before winter (n=10); in 2016-2018, when lynxes got common, the extremely high mortality in wolf pups was registered - 89% (n=11). For instance, in the warm season of 2017 in Naliboki Forest there were located 7 wolf litters, and in September-October only two pups were registered altogether (one pup in two wolf packs).

Concerning the breeding rate of wolves and pup survivalship in Naliboki Forest, it is important to describe about two individual wolves, which life stories were traced by us in a lot details. We think that the life stories of these two wolves are hard to call as typical ones, but undoubtedly that they reflect much reality of wolf reproduction in Naliboki Forest. One of the traced wolf individual was adult female, which failed in her breeding a lot. Another wolf individual was a supressed pup, which could overwinter alone without the large family of 15 wolves (ten pups, founding male, two mothers and two pup-sitters), in which it was raised.

First, we will tell about the unfortunate female wolf. This wolf female has been easily recognized by the tear in her right ear since February 2017, when we began to call her Torn Ear. Before that we recognized her by whitish stripes in the lower part of her head and black marks at the eyes.

Torn Ear life story. In Naliboki Forest since February 2013 Torn Ear has been registered living and reproducing in the wolf group of three breeding females and one or two adult males altogether. On 11th May 2013 we discovered three wolf litters in the dens within the small spot of spruce-black alder forest somewhere between the localities of Drazdy and Rabachova. The wolf dens that belonged to the three breeding female wolves were situated at the distance of about 430 meters, 220 meters and 380 meters between each other. The pups in one litter were about 40 days old, the second litter was about 15-18 days old, and the third one consisted of small blind pups. The first and second litters were mixed as: 2 pups of 40 days old and 2 pups of 15-18 days old; and as 2 and 3 such different age pups, respectively. It happened like that because the mothers stole pups from the dens of each other. None of the pups including the litter of Torn Ear survived by the winter 2013-2014.

During the breeding seasons of 2014 and 2015 we did not collect enough precise

information about the reproduction in this wolf group. At least, we knew that they bred and had pups till the late summer or autumn, but during the coming winter there were again five adults only without any pups i.e. three adult females and two adult quite big males. Sometimes, one of the males walked separately, but within the same territory of the other wolves of the pack. Again, sometimes we registered that Torn Ear walked separately with one of the males, while other two females stayed with another male within the same territory.

In April-May 2016 one or more females from the wolf breeding group that included Torn Ear gave birth in the Rabachova locality; there was registered minimum one litter. But all the pups disappeared by the end of May.

In February 2017 Torn Ear (when she was with a normal right ear) and other four members of the wolf pack were taken in a fladry enclosure in the localities of Kurhany and Symonava by the local hunters. That day, by driving there, we saw a number of vehicles and more than thirty hunters, who did the hunt-drive to kill the wolf pack. The hunter tried to do their bloody work during the whole day. Nevertheless, Torn Ear and other wolves escaped more or less safely from the fladry enclosure. One shot of hunter wounded the right ear of the female. Also one male wolf from the pack was wounded to the right hind leg, but he survived.

In the late April 2017 all three females of the wolf pack gave birth definitely. The distances between their initial dens were

(233, 234) *Torn Ear the female wolf in Naliboki Forest*

0.92, 0.72 and 0.95 km from each other. One male mostly looked after two breeding females including Torn Ear, whereas the other male took care about the third breeding female. Torn Ear was registered visiting not only own den, but also the den of another breeding female, to which the same male served. Interestingly that at one of the dens all these five wolves were registered altogether on 1st May. We documented that two litters were killed by adult male lynx that we called Jury. It happened in the end of April and the first days of May, whereas the third litter disappeared in the mid-June. In 10-15 days afterwards all the five wolves started walking widely within the previous winter home range and marking a lot.

After the clear documentation that the two wolf dens were extirpated by the adult lynx male we started thinking that all previous breeding failures of the wolf pack happened due to the same lynx male aggressivity.

In the late April 2018 the wolf breeding group consisting of Torn Ear, two more breeding females and still two adult males began preparing denning in the same Rabachova locality again. They prepared minimum 5 dens before any parturition. Everywhere in the places they stayed there were registered lynxes in the close proximity. Then suddenly before any giving birth

(235) *two of the five pups of Torn Ear the mother wolf in Naliboki Forest in June 2019.*

the wolf breeding group disappeared and they were not found in the whole Naliboki Forest during the summer. We hypothesized that they emigrated from Naliboki Forest to breed in the surrounding more rural area where there were not so many lynxes around because of the dramatic experience of the previous May, when Jury the lynx had killed all their pups.

After a long absence, Torn Ear with one of the males and one of the females was found to come back to their former territory in early March 2019. They were with another unknown third female, which could be a young adult (*i.e.* the one survived pup of the year). The area was already occupied by other three wolves. These

wolves were gradually sent away by the former owners including Torn Ear.

In late April 2019 Torn Ear and at least one more female of this wolf group gave birth. Torn Ear's den was placed in the Asovyja locality, while another female denned in the Rabachova locality. Their male served for both mothers, that together with their pups were situated at the distance about 3 km apart. Then since the mid May both mothers with their litters were registered on stay in the Asovyja locality. Another female's litter was situated in a badger outlier, where the pups were killed by a male lynx. We registered the tracks of the lynx entering the burrow-den and one pup remains 120 meters away of the den. The litter of Torn Ear was saved and in the beginning of July it consisted of 5 pups you may see in the photos below. Both females and their male took care about the pups.

The second above-mentioned life story of individual wolf tells about a pup, which appeared alone without parents and faced with the harsh winter conditions. Nevertheless, it has survived by passing through many dramatic events. We called the wolf pup Sirotka that in Belarusian language means an orphan. We think that Sirotka is a male, but it is only a guess.

Sirotka life story. Sirotka was raised in the Valiavatka locality of Naliboki Forest within a big family of wolves that consisted of the father, two relative mothers (the breeding mother and her breeding daughter), two litters of the two mothers having ten pups altogether and the two pup-sitters. These two pup-sitters were subordinated by the parents from non-breeding and non-relative females roaming around.

In early September this large wolf family was discovered by unknown hunters and they tried to extirpate them. The wolf family was sheltering in high dense grass stand in the Vol'ka small river valley, from where it was hard for the hunters to push them out. In particular, the pups stayed in the grassland surprisingly sticky. Hunters used strong alarm, but succeeded to scare and push out the adult wolves only. The pups still remained in the grassland.

After the hunter attack the adult wolves were afraid to join with the pups for at least three days. Every of these days big male lynx, which we called Bazyl', was present around the pup refuge in the grassland. We registered Bazyl' by camera traps as well as by his tracks on the sand dunes nearby. Actually Bazyl' was present around the wolf family during the whole summer, perhaps, trying to kill the pups, but the pup sitters were around all the time. It looks like during that time, when the adult

wolves were absent, Bazyl' lynx killed six pups. Then the adult wolves came back to the pups in the grassland, but there were already only three of adults: father, one mother and one pup-sitter. Perhaps, another mother and one pup-sitter were killed by the hunters. The returned adult wolves had collected the four survived pups and moved to another place in the Valiavatka locality. This new place of the pup stay was situated about two kilometers from the previous one.

That Valivatka house area was well-supplied with prey, and the family stayed there till the mid-October. The adult wolves succeeded to kill a stag red deer and male elk in the proximity to the new house spot of the family. Since the mid November the wolf family began ranging a lot faraway from the house spot. During this time just before overwintering the wolf family hunted and re-established the home range, which the parent wolves used during the previous winter.

(236) *Sirotka the wolf pup in Naliboki Forest*

One of the pups was evidently suppressed by others, and it was always left to stay in the Valiavatka house area, perhaps feeding on the remains of the killed deer and elk. Also, the lone pup caught small rodents in the grassland of the Vol'ka river valley.

From time to time the wolf family returned to the Valivatka house area and joined with the lonely staying pup. Once after a night snowfall the wolf family was got in fladry by hunters somewhere faraway from the Valiavatka house area, where all of them were killed. The poor pup, which we started calling Sirotka (i.e. an orphan), appeared alone within the inimical forest. Approximately for a month Sirotka was feeding on the poor remains of the deer and elk as well as trying to catch small rodents. Also, Sirotka excavated many bones that were hidden by him or other pups in the Valiavatka house area before. Sirotka gnawed the bones a lot trying to

(237) *Sirotka's family that was extirpated by hunters in December of 2018 in Naliboki Forest. The photo was provided by one of the hunters, who took part in that killing of Sirotka's family.*

consume something digestible. For a month Sirotka stayed mainly in that small home spot of about one square kilometer, and sometimes it tried go outside of this house area.

Perhaps during one of such a walking Sirotka was subordinated by a pack of stray dogs which stayed like a wolf pack in the forest in the localities of Dushilava, Stashikha and Patashnja. Sirotka persisted a month together with them in those localities that was maximally about ten kilometers away from the Valiavatka house area. Then perhaps it was sent away and came back to the former house area in the Valiavatka locality.

After coming back to the house area Sirotka began feeding again on very poor remains of the elk and red deer carcasses as well as he excavated bones (there were surprisingly many of them!) that were cashed before. Also, Sirotka well learned catching of rodents and, actually it lived as a red fox between foraging on rodents and scavenging for carrion. In March its fairly big scats consisted of ungulate bone remains and hair of small rodents. Finally, Sirotka has survived almost alone till spring. Surprisingly, but it is true. However, the Sirotka did not grow enough, and in April it was the same size as in November that is something between a small wolf and a big red fox.

In May Sirotka was still alone and began living on the larger area about ten square kilometers. Sirotka started marking tensely its area by stating that it is its property. The Valiavatka house area was just the occupied territory center.

So, by concluding, it may be stated that the above-presented data and the story information about survival of wolf pups in Naliboki Forest again suggest about the crucial role of lynx predation for survival of wolf pups. It is becoming evident that, when in a forest massif the lynx gets a high population density, the local wolf population appears in a "trap" due to reproduction "pit-fall". Here it is worthwhile to notice that in Naliboki Forest within the mentioned three periods, when the population density of lynxes increased a lot, the numbers of inimical for wolf reproduction ungulates such as stags and bison first of all grew markedly. That added problems for reproduction in wolves of course.

The reproduction problems in wolves are based not only on just the lynx interference towards wolves, and also on the manner of wolves to raise pups with leaving them for quite long in a sheltered site, when the parent wolves go for foraging. Thus, wolf pups like exposing for an easy

killing by lynxes. Since the lynx-related problem in the wolf reproduction in a forest massif appears, the local wolf population becomes persisting not due to reproduction, but because of immigration from adjacent rural-forest mosaic terrains, where pups survive easier with a few or no lynxes in the habitats.

It looks like such a declining situation in wolves (*i.e.* the reproduction "pitfall" in forest massifs) was not forever. Lynxes as well as wild ungulates were not so common in the primeval forest on the territory of Belarus in the Middle Ages, *i.e.* in the Great Lithuania. Indeed, there are not so many mentioning about lynxes in the game documents of 17th-19th centuries for Naliboki Forest and the central Belarus on the whole, whereas wolves were mentioned at the same time a lot (Belarusian archive departments 694, chapter 2, and articles 201, 1587, 3984, 4353 in it and chapter 3, and articles 2012, 2015, 1217; Zavisha, 1862(2011); Niamtsevich, 1868; Shyshyhina-Patotskaya, 2007). As far as we can realize from the historical documents there were markedly fewer lynxes in the more primeval forest – approximately 1-5 inds per 1000 km^2.

Then the intensification of logging with early reforestation on clearcuts conditioned markedly higher habitat carrying capacity for wild ungulates and lynxes. Lynxes got manifold (about ten times) commoner, and frequency of wolf-lynx interference increased a lot. Thus, we hypothesize that just logging is responsible for such situation of the reproduction "pitfall' in wolves that inhabit forest massifs.

The material that we obtained through the age determination of wolf skulls can bring some more knowledge on the survival in young wolves. Table 6.2 represents data on the age composition in slightly and heavily controlled wolf populations in Paazierre Forest, and these data provide possibility to assess survival of young wolves between 6 to 18 months. The ratio of the yearling number over the juvenile number suggests that the survival in young wolves aged from 6 to 18 months constituted about 0.62 in the period of fairly low hunting pressure. When wolf persecution by human became heavy, the survival in young wolves aged from 6 months up to 18 months was markedly lower (0.28) than that after the period of fairly low hunting pressure ($G=13.2$, $P<0.01$). So, winter mortality in wolf pups in Belarus is determined a lot by the pressure of wolf persecution by human.

In the question of mortality in wolf pups, there is another important aspect that is tightly connected with multiple breeding

in a wolf pack. In most cases sometime in July-September one of the mother wolves begins to live alone with its pups after its sending away by another stronger mother wolf. Quite often the expelled mother is young (2+ only or even 1+ sometimes) , and such a young mother is not able to hunt good enough to feed itself and the pups. Also, it is hard for such a vulnerable mother to establish own territory alone. Therefore, such weakened wolf pack mostly scavenges around villages, kills dogs, takes carrion and try to hunt domestic ungulates. We traced four stories of such wolf packs of young mothers and their pups. Concerning these four mothers, it looked like two of them overwintered, other two were killed. Concerning their pups, only 2 out of 20 of them that were registered in November-December could overwinter, and their winter survival was about 10% only. Also, it is worthwhile to notice that all these four packs lived in the conditions of presence of a few lynxes in the habitats. Perhaps, if lynxes were common, the stories of these packs might be even worse.

6.2. Decline in the wolf reproduction with implication for wolf pack composition

In Naliboki Forest, when lynxes got common since the autumn of 2015 (more than 40 inds) and additionally there were appeared too many wild ungulates that are inimical for wolves at denning (first of all, red deer stags and bison), the reproduction in wolves almost stopped due to disappearing most of the pups.

In turn, and family-origin pattern of wolf packing was substituted for subordination-origin one. As you learnt from the previous item, the disappearance of wolf pups is strongly connected with the deliberate predation of adult lynxes (in particular males) on wolf pups. Also, wolf pups are trampled by wild ungulates that live in close proximity.

With respect to this it is worthwhile to compare the wolf number, portion of pups in the local wolf population in Naliboki Forest in November-December (when pups are still recognisable), patterns of wolf pack forming in October-January. As to a pattern of wolf pack forming, it is either family-origin, *i.e.* parents with pups or subordinating pattern , *i.e.* a strong wolf has subordinated other wolves that ranged around.

(238) *Wolf pack that consists of adults only (Naliboki Forest, November of 2017).*

In early winter of 2008-2012 in Naliboki Forest and its forest-agriculture surroundings in the area about 2700 km^2, there were 51-70 wolves . In the beginning of winter the portion of pups of the year (0+) was 25-44%, and 86% of the investigated packs were of family-origin. Actually, some of such packs included a few non-relative subordinated individuals, but anyway the main partern of wolf pack formation in Naliboki Forest was family-originated.

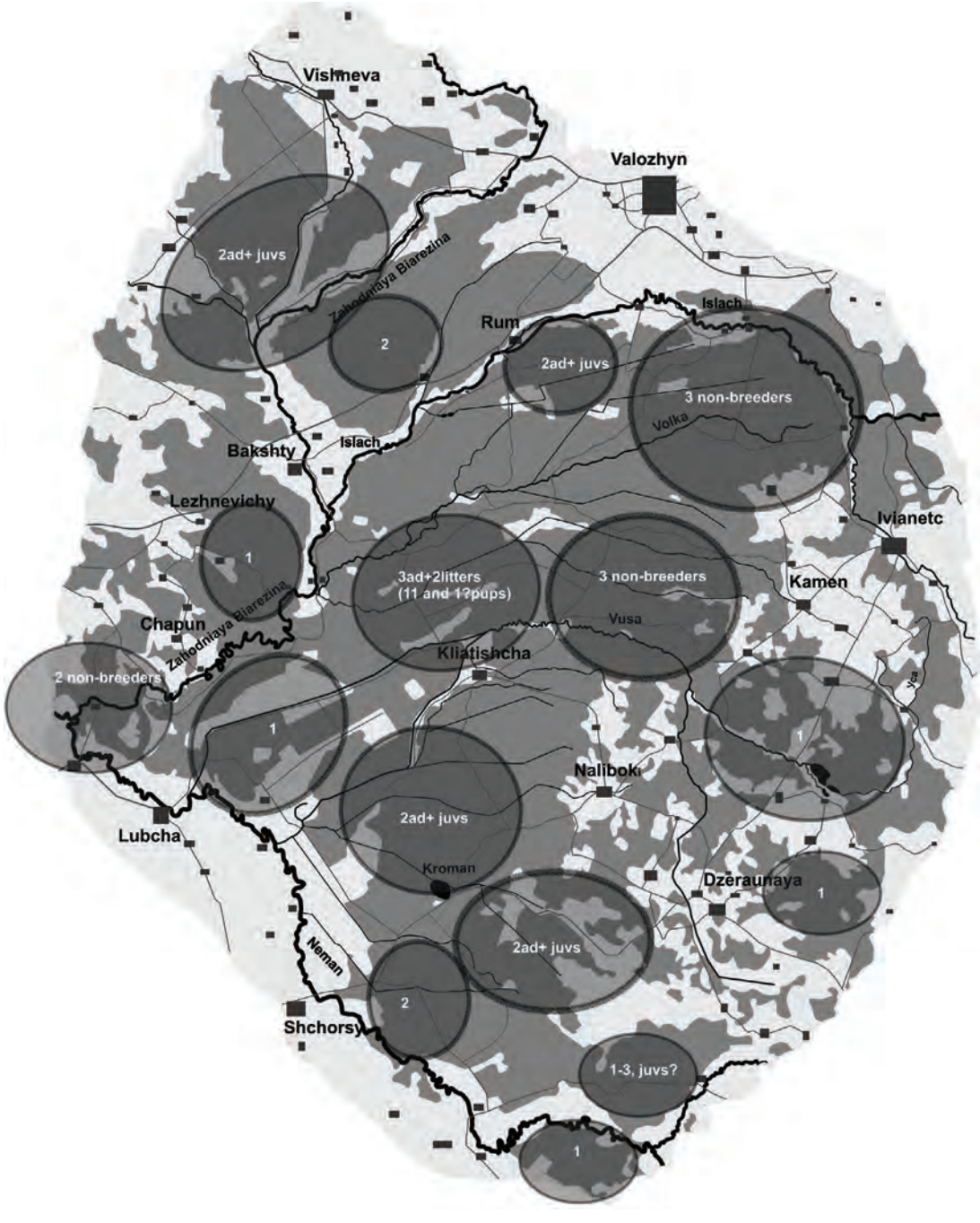
In early winter of 2015-2019 on the same area in Naliboki Forest and its forest-agriculture surroundings, there were 26-44 wolves. The portion of pups of the year (0+) was 14-18% and the majority of the packs (at least, 69%) were entirely or mainly of non-family origin, *i.e.* mainly consisted of non-relative subordinated individuals.

Thus, in 2008-2012 the local wolf population in Naliboki Forest existed being supported by its reproduction, while nowadays in 2015-2019 it still exists due to the immigration of adult wolves during mating season. It becomes evident from the detailed mapping of the local wolf population in Naliboki Forest in the period from May 2015 till October 2017 (Maps 6.1-6.8; see the comments).

As you see on the wolf distribution maps nowadays the pup survival is very low: After 6 or 7 litters in May 2015 there were registered only 4 pups in the late November 2015; only 6 pups of the year were registered in the early winter 2016 after 10 litters altogether that were registered in May 2016; from the 7 litters that were traced during summer 2017 only two pups survived till October 2017. In 2016-2017 during January-February many wolves arrive in Naliboki Forest (almost as many of them as there were lived). Then in the late March and April an essential part of the wolf local population (perhaps, mostly breeding pairs) emigrated from Naliboki Forest, because of the habitats were occupied by either other breeding wolves or lynxes. Before 2016 the wolf population in Naliboki Forest was considerably more stable and the family-origin pattern of wolf packing prevailed (Sidorovich, 2016).

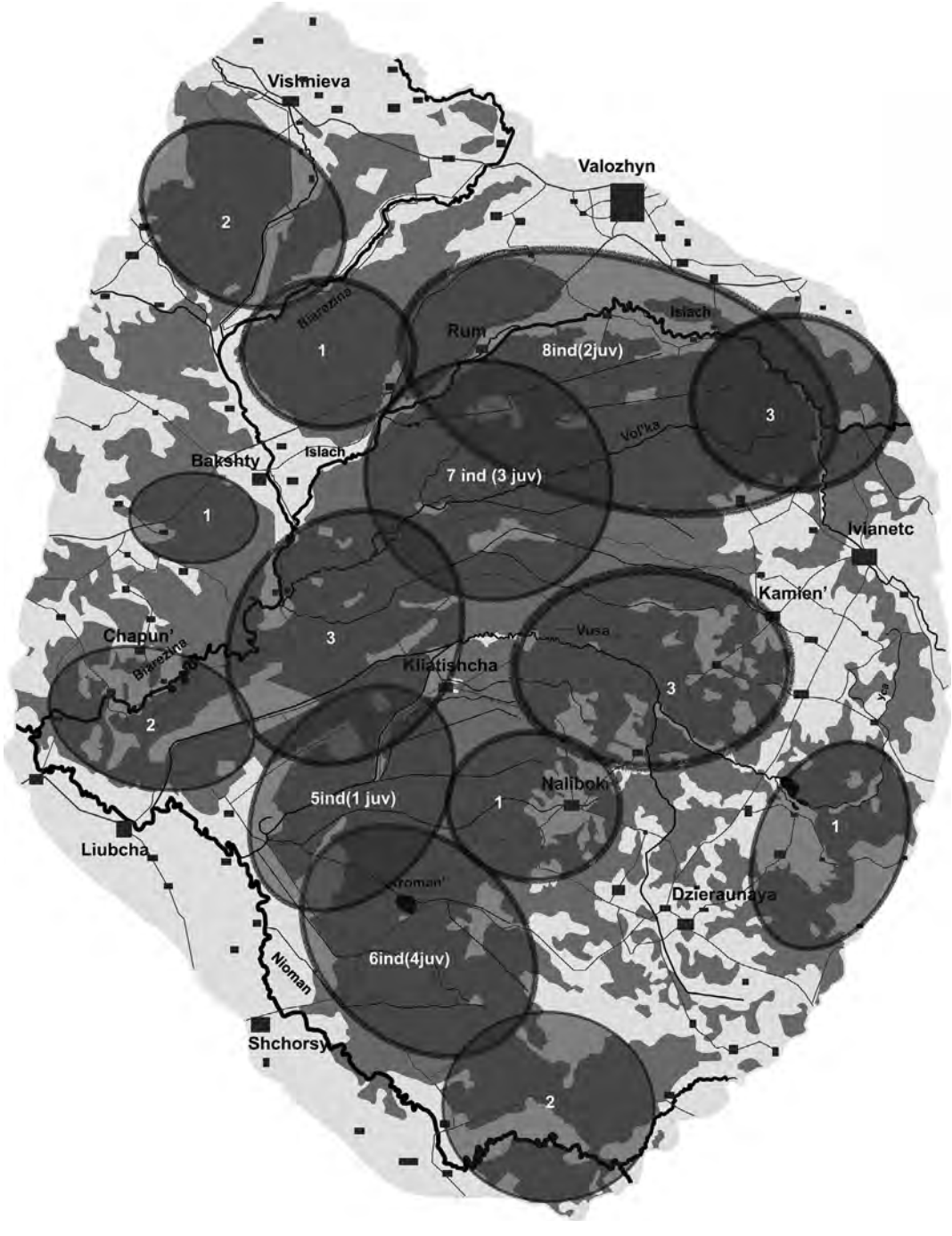
Concerning the wolf situation in 2018-2019, that was principally the same (see Maps 6.9-6.12) as in 2016-2017. In the end of 2017 (late December) in Naliboki Forest we censused 42 wolves, and there were 4 pups of the year. At least, a third part of them (we heard about 13 hunted wolves) were killed by hunters till February. Anyway, in February of 2018 the number of wolves in Naliboki Forest approximately varied from 70 to 90 individuals (mostly adults arrived for mating). Then in March there were censused 66 wolves. In April it was evident that in Naliboki Forest there were 24 breeding couples and larger groups of wolf breeders up to 5 (see Map 6.11). Most of them emigrated from Naliboki Forest during the second half of April. In May-July of 2018 in Naliboki Forest during the intensive study on wolf denning there were registered 29 adult and subadult wolves and 4 litters of two breeding groups. Additionally, pups of one more breeders disappeared in early days.

In the early December of 2018 in Naliboki Forest there were only 22 adult wolves and 4 pups of the year. Again 10 or even 14 of them were hunted till February, whereas in February and March of 2019 the number of wolves in Naliboki Forest approximately varied from 50 to almost 80 individuals (mostly adults arrived for mating). Then in late March and the first half of April there were censused 67 wolves mostly in 25 breeding couples and larger groups of wolf breeders up to 4. Again, in May-July of 2019 in Naliboki Forest during a lot of investigation of wolf denning we found that in the terrain there were denned only 4 breeding groups: two single breeding and two double breeding; 6 litters altogether. Till July we got much that already one wolf litter was killed by bears, and another one was extirpated by lynx. Besides pups there were registered 23 wolves.

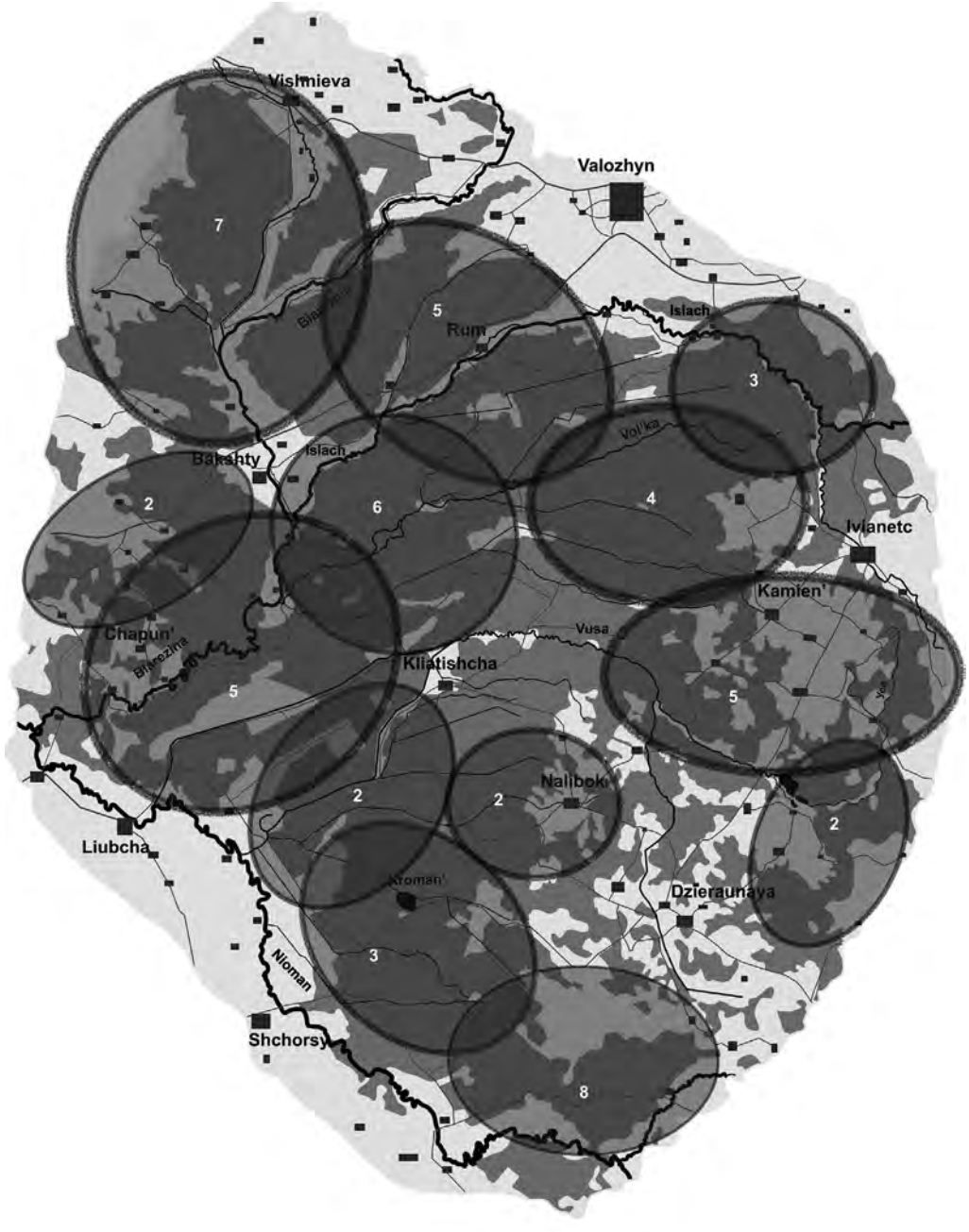


Map 6.1. Wolf local population in Naliboki Forest and its surroundings in May 2015 (slightly corrected in June). There were censused about 31 adults and subadults; definitely 6, but plausibly 7 litters were located.
Comment: After these 6-7 litters in May 2016 there were registered only 4 pups in the late November 2016.

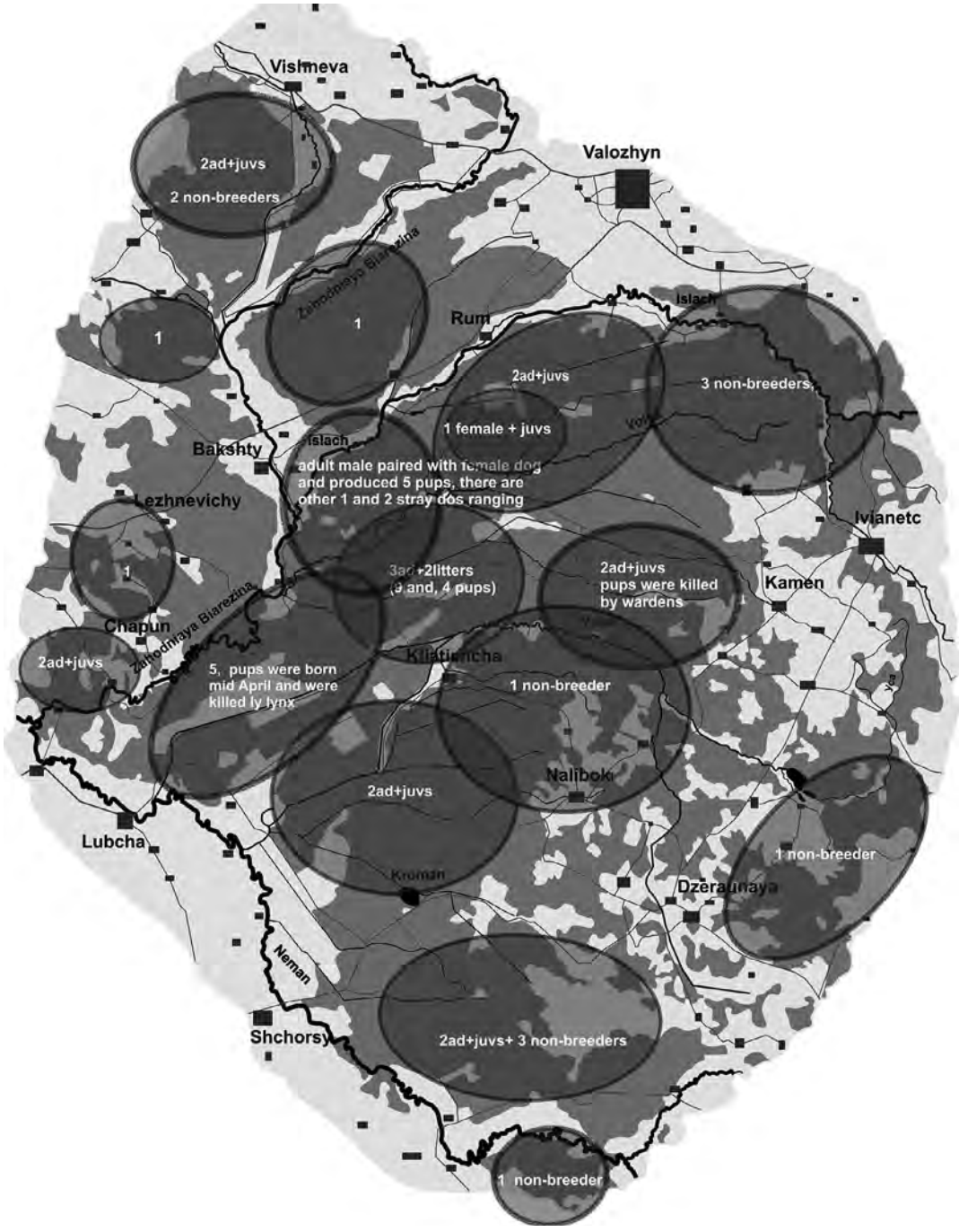
Map 6.2. Wolf local population in Naliboki Forest and its surroundings in the late November and early December of 2015. There were censused 26 adults and subadults and only 4 pups of the year.
Comment: it is after 6-7 litters in May.



Map 6.3. Wolf local population in Naliboki Forest and its surroundings in the late January 2016. There were censused 34 adults and subadults and 10 pups of the year.
Comment: since the early December two packs of 8 inds (including 2juvs) and 6 inds (4juvs) arrived, one lone wolf dissappeared, and in the north-east of Naliboki Forest 3 individuals appeared instead one.

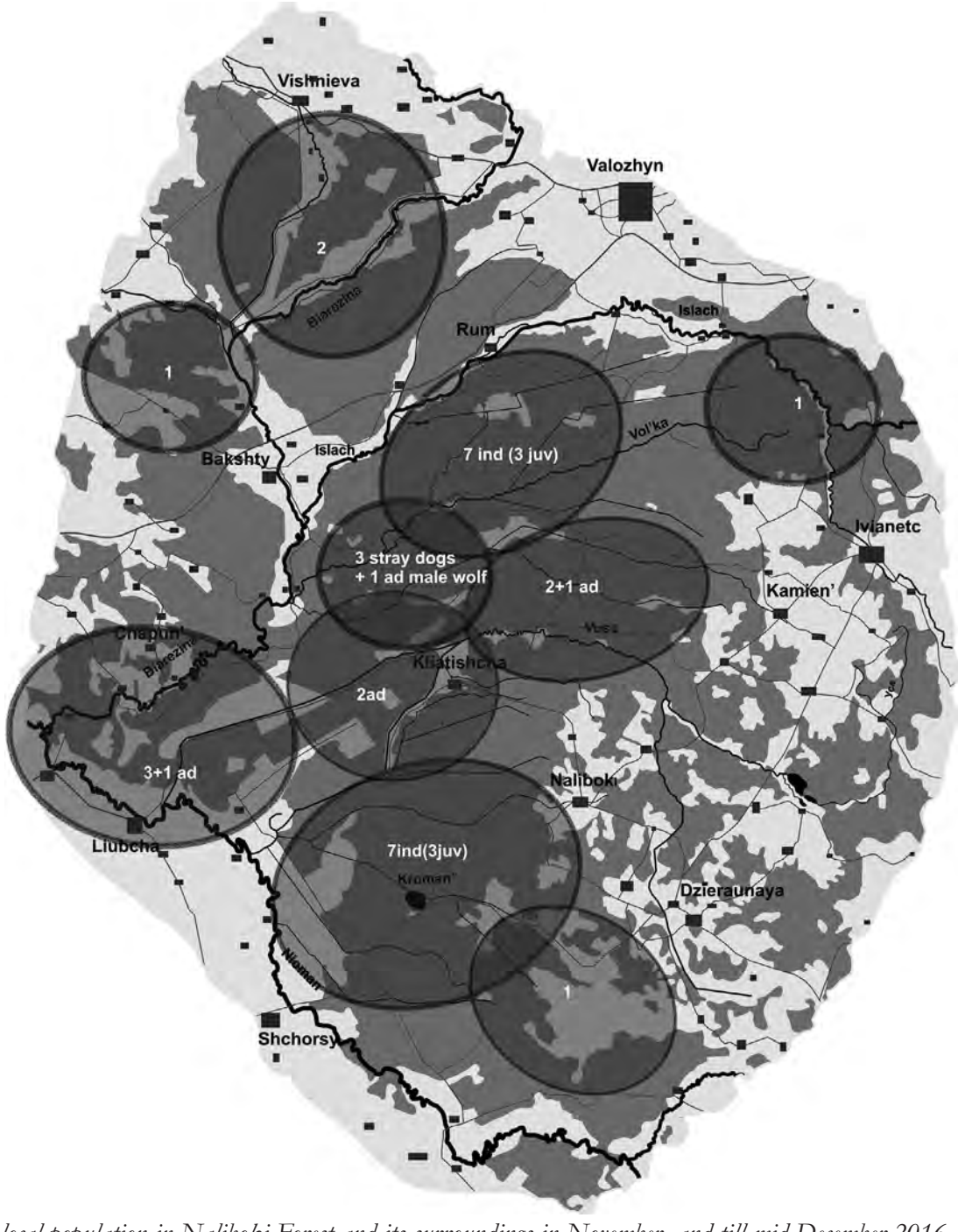


Map 6.4. Wolf local population in Naliboki Forest and its surroundings in the early March 2016. There were censused 54 individuals.
Comment: it is 20 individuals more that in the late January, despite in February there were killed 5 wolves in the central east of Naliboki Forest, 5 wolves in its south-east part, and 5 wolves in the central-west of Naliboki Forest. So, about 35 wolves arrived in Naliboki Forest in February during the mating season in wolves.

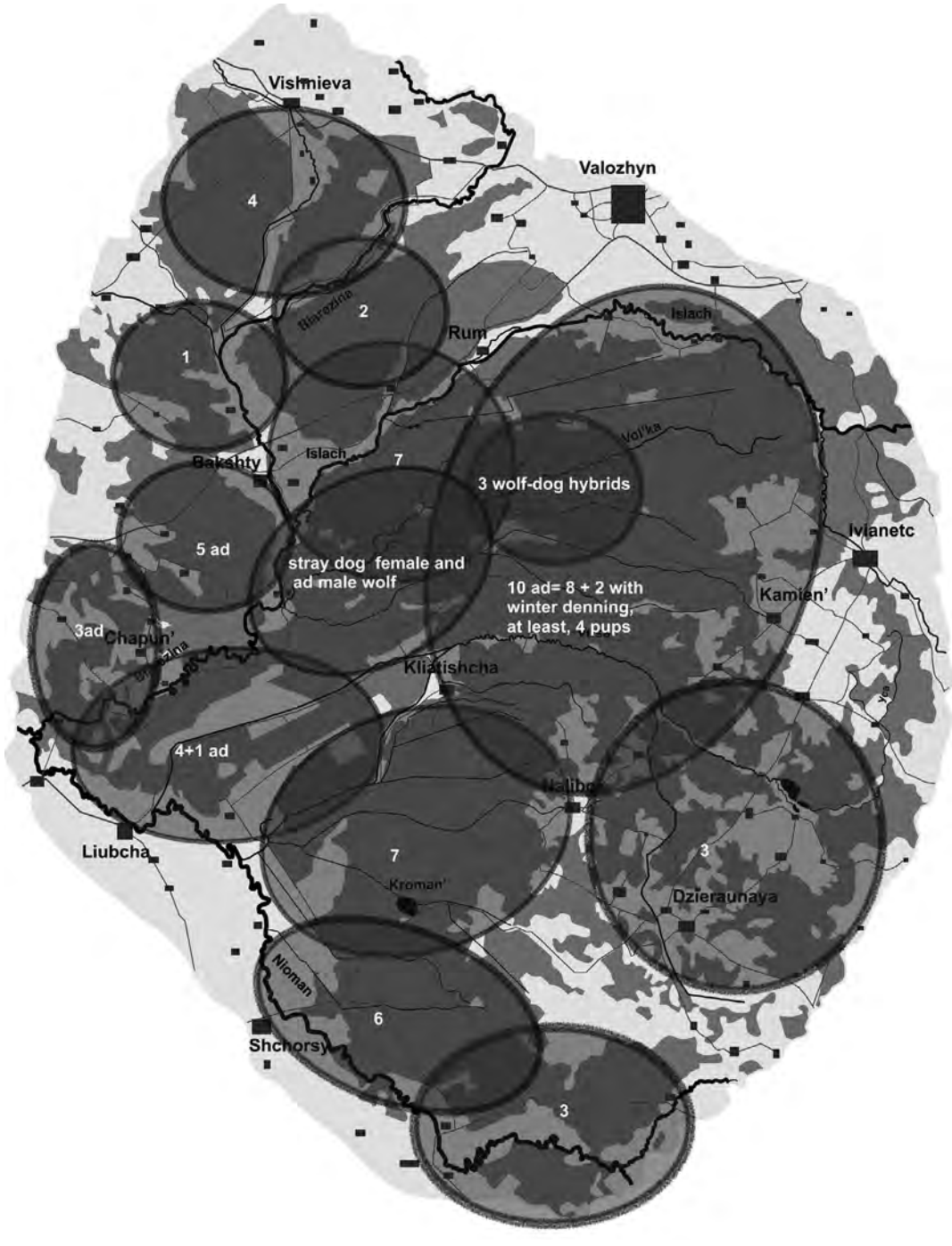


Map 6.5. Wolf local population in Naliboki Forest and its surroundings in May 2016 (precised in June). There were censused 36 adults and subadults; 9 wolf litters were located, additionally one litter was killed by lynx and there was one hybrid wolf-dog litter.

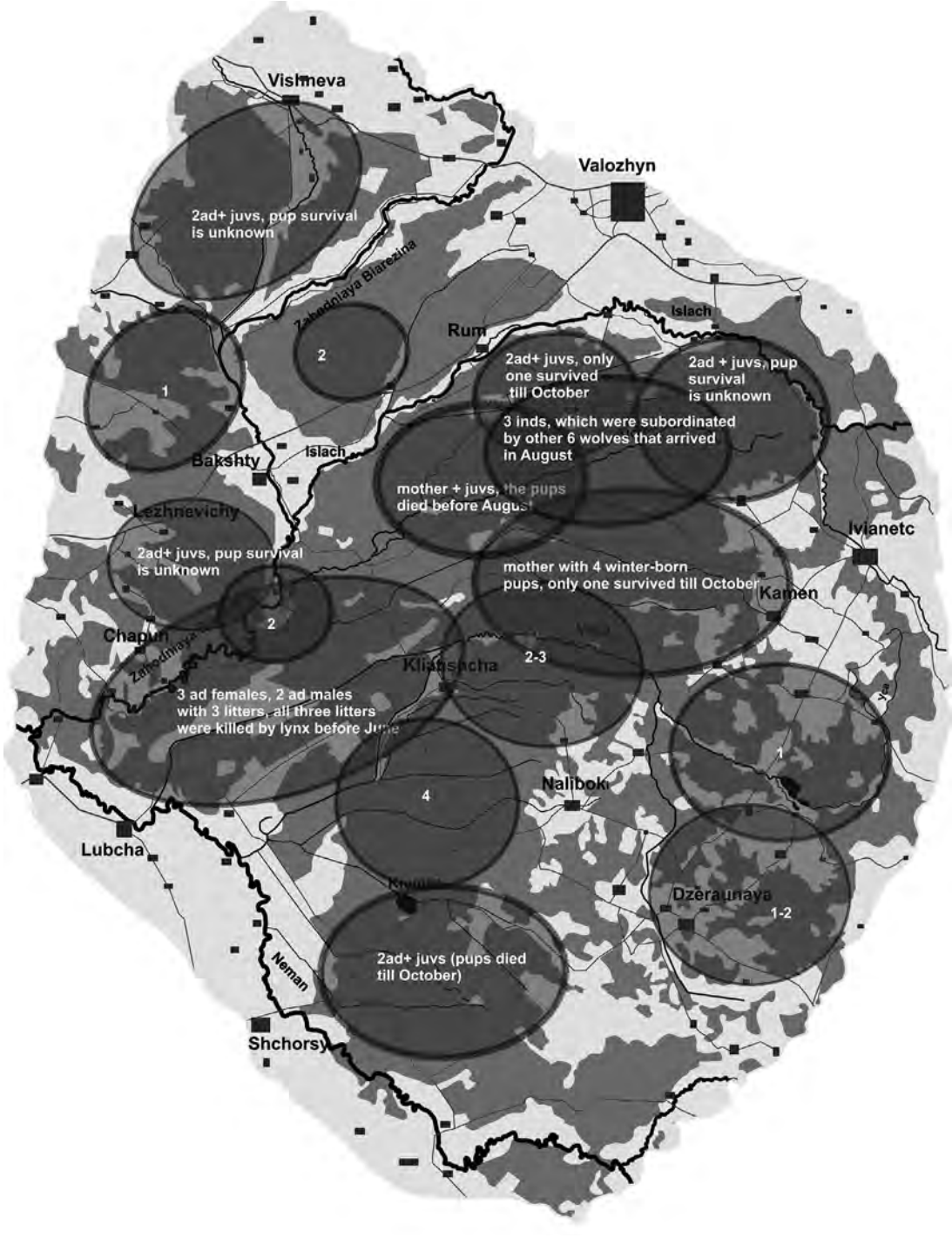
Comment: it look like a part of breeders had emigrated; it becomes evident, while comparing the May situation with one in the early March, when there were registered 54 wolves.



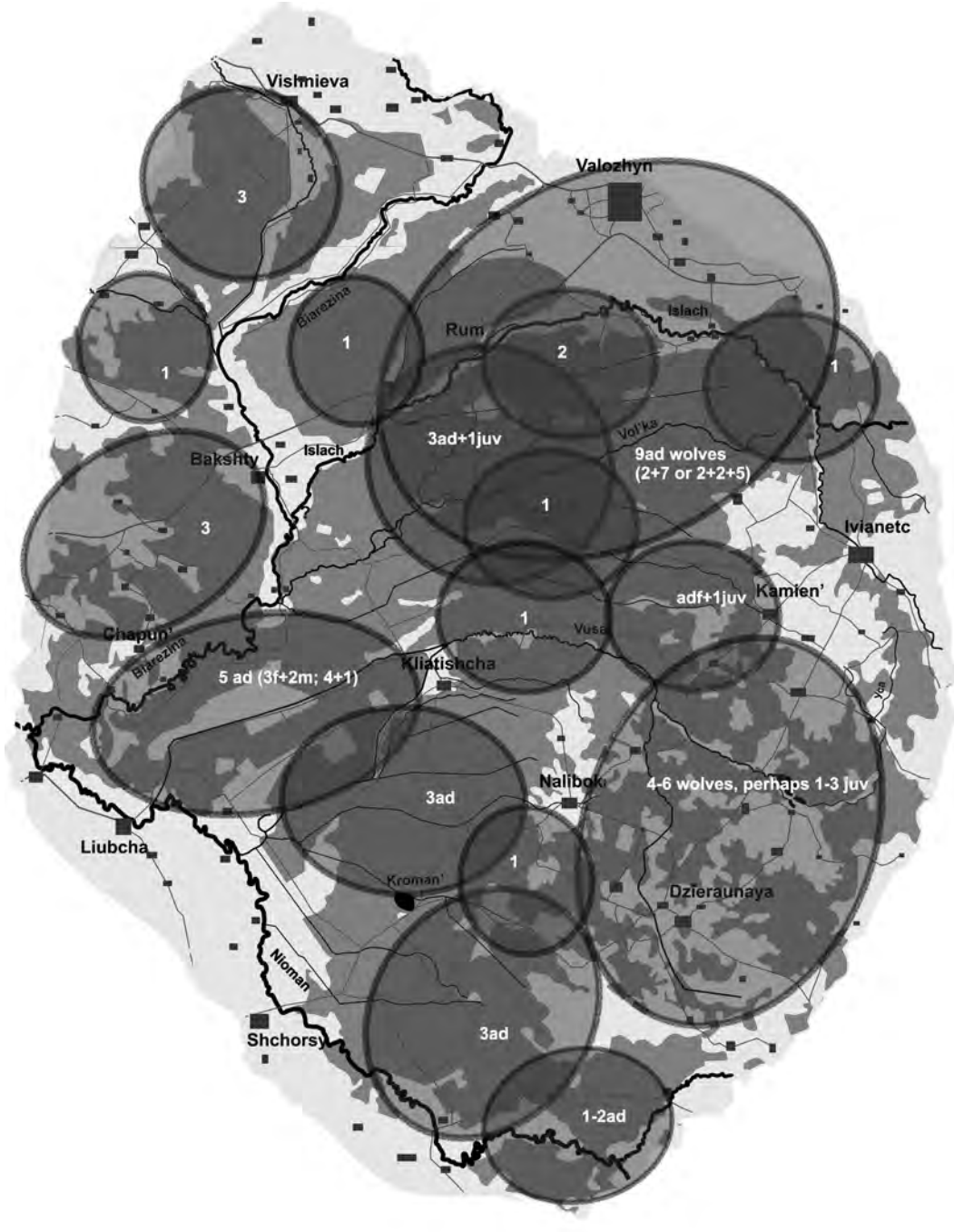
Map 6.6. Wolf local population in Naliboki Forest and its surroundings in November and till mid-December 2016
There were censused 23 adults and subadults and 6 pups of the year.
Comment: there were only 6 pups of the year after 10 litters altogether in May 2016.



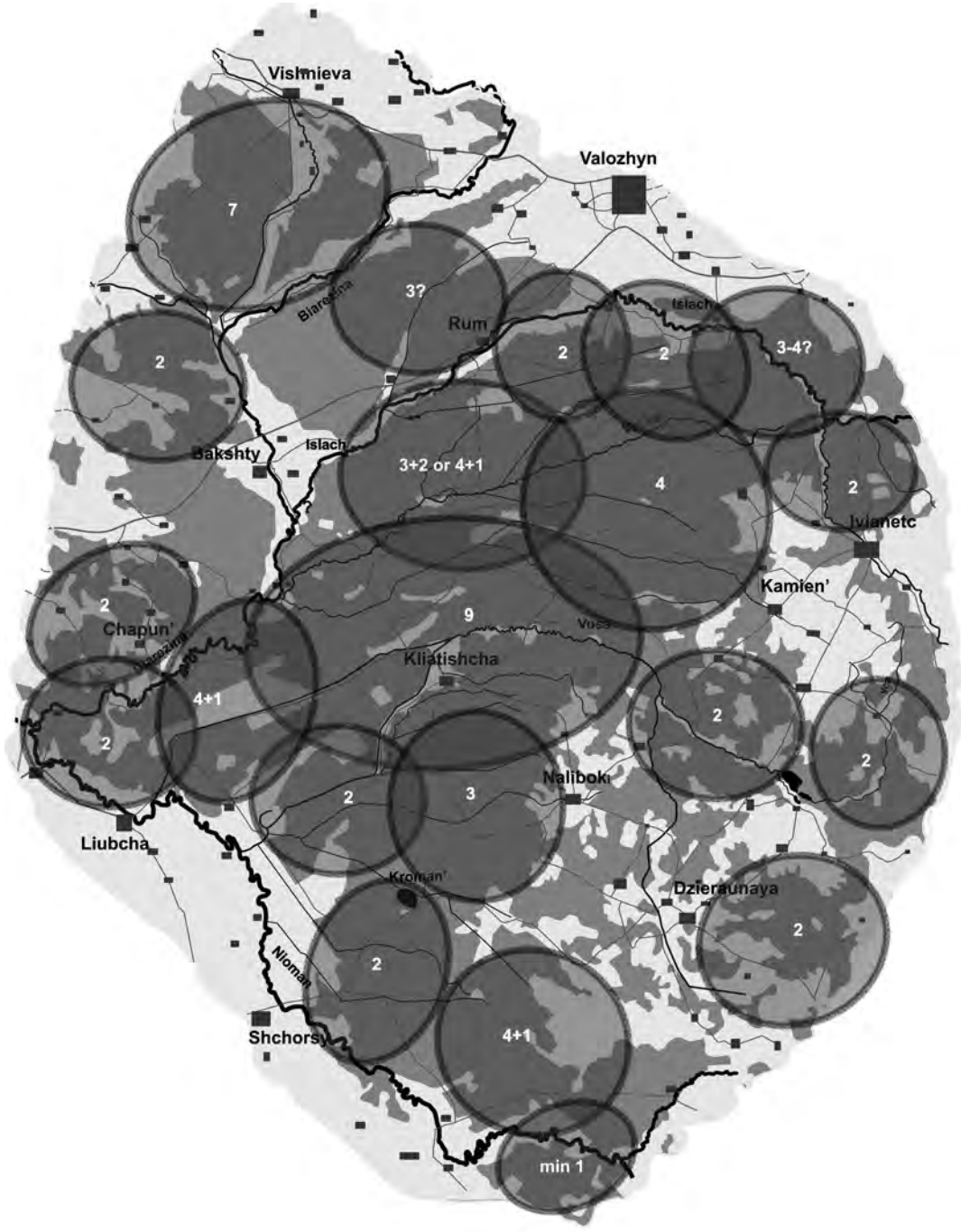
Map 6.7. Wolf local population in Naliboki Forest and its surroundings in late February 2017. There were censused 57 wolves.
Comment: it is double number of wolves compared to the that in Naliboki Forest in the late November despite of, at least, 7 wolves were killed in December-January.



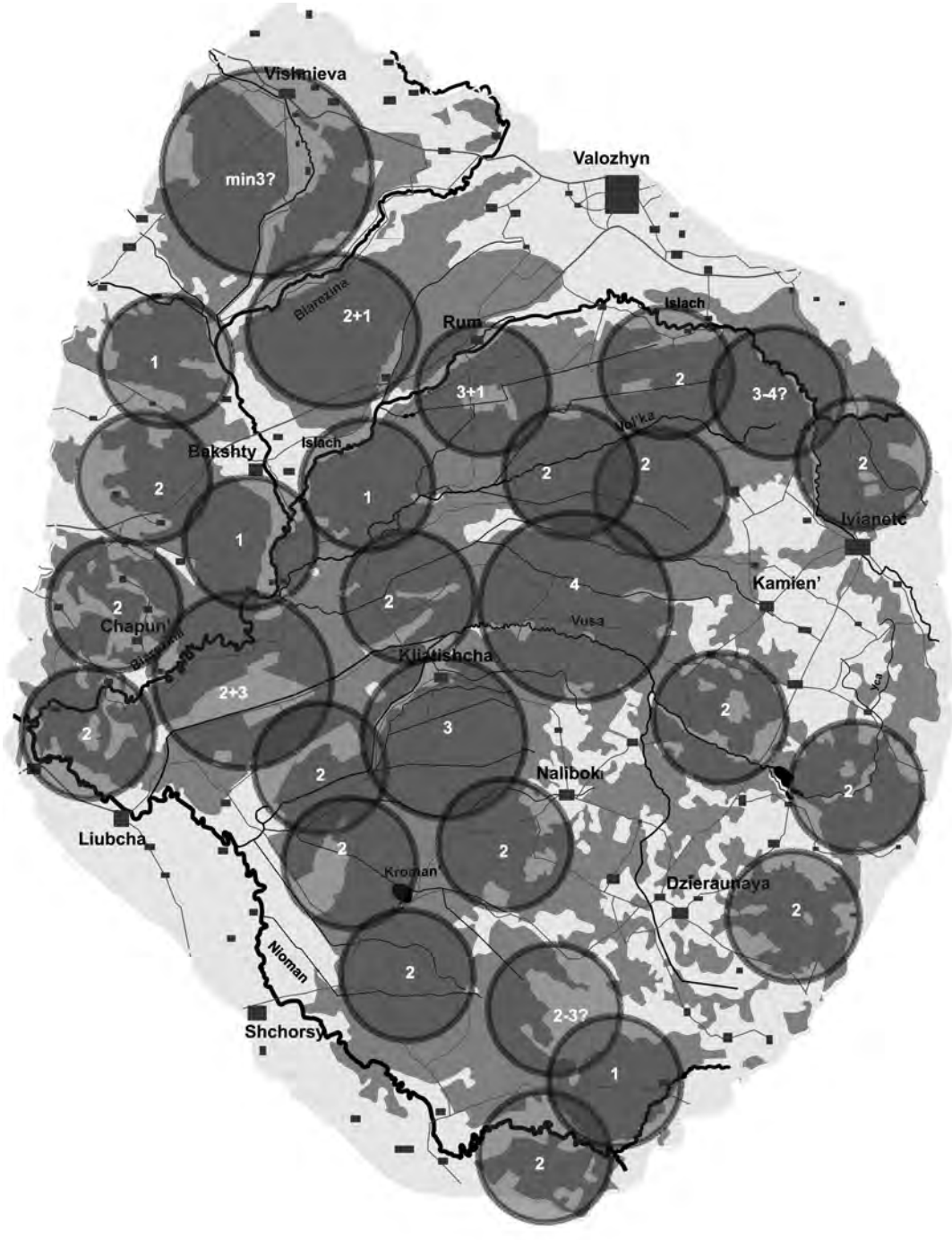
Map 6.8. Wolf local population in Naliboki Forest and its surroundings in May-October 2017. In May there were censused 35 adults and subadults, and 9 litters were located. Three litters were killed by lynx before June.
Comment: the number of adult and subadult wolves decreased greatly since February. From the seven traced litters only two pups survived till October.



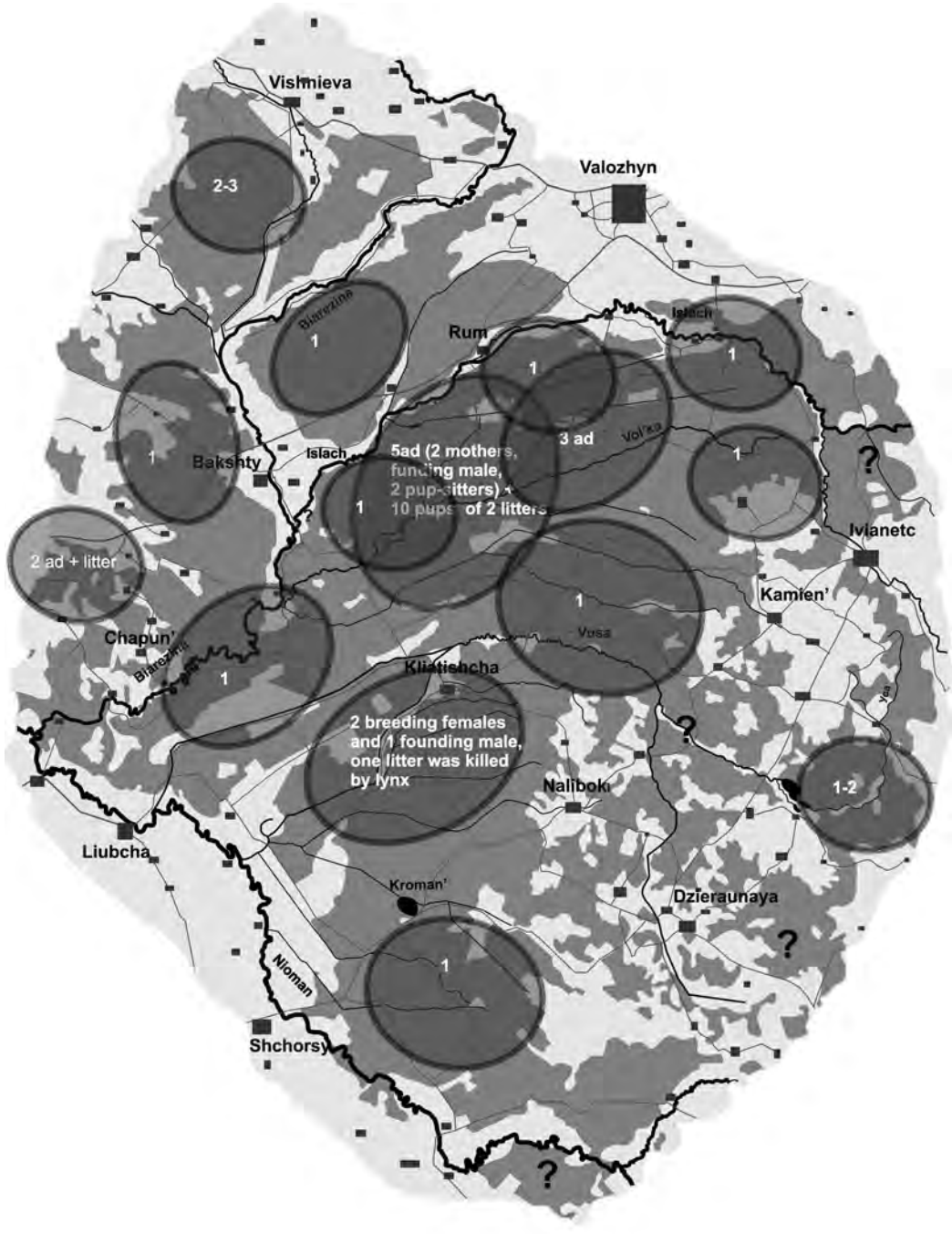
Map 6.9. Wolf local population in Naliboki Forest and its surroundings in November and December 2017. There were censused 42 adults and subadults and 4 pups of the year.
Comment: only 4 pups of the year after 9 litters altogether in May.



Map 6.10. Local wolf population in Naliboki Forest and its surroundings in early March 2018. We censused 66 wolves. Comment: 24 wolves more compared to November-December 2017, despite of the fact that, at least, 13 wolves were killed in December-January.



Map 6.11. Local wolf population in Naliboki Forest and its surroundings in early April 2018. We censused 24 potential breeding groups of wolves (plausibly having pregnant females) and 59 wolves altogether.



Map 6.12. Local wolf population in Naliboki Forest and its surroundings in May-July 2018. In May we censused 29 adults and subadults, and 4 litters from two breeding groups were located. One litter was plausibly killed by lynx before June.
Comment: the number of wolf breeding groups decreased greatly; from 24 in early april to 2-3 in May.

Chapter 7. Trends in the denning behaviour of wolves in connection with the changes in the vertebrate community in Naliboki Forest

By investigating the denning behaviour and ecology of wolves in Naliboki Forest during the last years (2016-2019), we faced not only with the dramatic changes in the origin of a pack and its composition, but with several other evident trends in breeding behavior of wolves. That we connect with the changes in the local vertebrate community or more specifically with the pronounced changes in the population densities of those already mentioned species that may affect the denning conditions for wolves.

Here one more time we list briefly these changes in the local vertebrate community. The first change in the local vertebrate community is that during the last years, Naliboki Forest appeared to be densely populated by lynxes: (since 2015 more than 40 inds and in 2018 more than 80 inds. In 2018, the lynx population density in Naliboki Forest constituted about 5 inds per 100 km². This rather high density of lynxes was plausibly determined by very favourable habitat conditions in Naliboki Forest. There are still many old forest patches and simultaneously many clearcuts, whereas most of the numerous drainage canals are blocked by beaver dams. All such habitats are densely inhabited by roe deer, red deer, beavers, hares, grouses and ducks, and they are suitable prey for lynxes.

As it was suggested before, adult lynxes tend to deliberately hunt wolf pups and kill heavily pregnant female wolves; and in effect, the reproduction in wolves may stop, which has already happened in Naliboki Forest.

The second change is that during 2015-2018 the number of other vertebrate animals such as bison, elk and stags (i.e. relatively big red deer males) increased markedly in Naliboki Forest. These animals are usually aggressive towards wolf pups and wolf denning in general. In the spring of 2018, there were not fewer than 100 bison in Naliboki Forest, and approximately 20-50 stags per 100 km² and 40-80 elks per 100 km².

Also, during the last decade, up to ten brown bears appeared in Naliboki Forest, and that plausibly has a negative impact on wolf denning as well.

In these unfavourable conditions for wolf reproduction in Naliboki Forest the mortal-

ity in wolf pups until their first winter became higher than 90%, and in turn, the wolf packs in the terrain began consisting mainly of adults. Also, despite almost a double decrease of the wolf numbers in Naliboki Forest, the number of wolf breeding units (couple or larger group of breeding wolves) markedly increased – approximately 18-25 breeding units in the last years versus 7-13 before. Nevertheless, as that was already shown during the last denning seasons only a small part or even only a few of such breeders stayed in the forest for denning and raising of small pups. The majority of wolf breeders seemingly emigrated outside of the forest massive for denning, in order to save their pups, because Naliboki Forest is densely populated by animals inimical to wolf denning.

In Naliboki Forest we have already noticed this trend (i.e. emigration of breeding units of wolves before denning) in 2016 and 2017. However, in May 2016 and 2017 it was not so pronounced as in May 2018, when only four breeding groups of wolves out of 24 wolf breeding units registered in late March and early April remained in the forest massive for denning. Again, in May of 2019 in Naliboki Forest there were denned only 4 breeding groups (two single breeding and two double breeding; 6 litters altogether), while 25 wolf breeding units were censused in late March and early April.

We are sure of these results. From two to five of us worked for 40 days since the end of April until the 8th of June, and we discovered only 9 dens from one wolf breeding group consisting of two breeding females and one male. Before the unfavourable situation for wolf denning described above, we (one to three of us) worked for 25-30 days and found several hundreds of wolf dens including 2 to 5 actual ones i.e. with pups. At that time there were usually only 8-13 wolf breeding groups in mid-April.

Thus, the first trend in wolf denning behaviour in the new unfavourable situation in Naliboki Forest is emigration of breeders out of Naliboki Forest to den in the forest-agriculture mosaic surrounding the forest massive. There the majority of residential wolves are killed each winter during the species population control actions. Intensive camera-trapping in Naliboki Forest in 2015-2019 suggests that, at least, a part of such emigrated breeders comes back to their previous territories in the next autumn, but still it is hard to say what the reproductive efficiency of such breeders is. Actually, still we documented only three such cases (wolves are not easily recognisable by camera-trap-

ping), and in one of the three cases the returned pack of 9 wolves had 3 or 4 pups of the biological year, and in another case among the 4 returned wolves there was one pup of the year.

The second trend in the denning by wolves in Naliboki Forest is the increasing use of pine stands as a main denning habitat type. During the first decade of the 2000's and early 2010's only about 6% of the wolf dens, which were found by us (n=736 dens, mostly without pups, recent ones from were pups were recently relocated), were situated in pine stands or pine-spruce mixture. That time the main denning sites of wolves were in treefalls, young spruce thickets in clearcuts with early reforestation and abandoned badger setts, and 81% of the mentioned 736 wolf dens were registered in these three habitat elements. Quite opposite, in the new denning-unfavourable situation for breeding wolves in Naliboki Forest since 2016, about 52% of the found wolf dens (n= 104, again mostly without pups, recent ones) were situated in pine stands or pine-spruce mixture with poor forest floor. This switch in the used denning habitats by wolves may be explained merely by potentially less disturbance of breeding wolves by wild ungulates and lynxes in pine or pine-spruce stands with poor forest floor. These habitats are poor in food and poorly structured and thus markedly less frequently used by red deer, bison and lynxes that are hazardous to denning wolves.

During the breeding of wolves in May 2019, when the number of red deer and bison increased even more in comparison with May 2016-2018, it was found that all 51 wolf dens (3 active dens with pups and 48 already abandoned dens due to relocating of pups) from four investigated breeding groups of wolves were situated in pine or mixed pine-spruce stands on dry lands almost without fallen trees and with poor forest floor. In such forest patches there were registered the minimal abundance of tracks of wild ungulates, while all known treefalls were densely occupied by red deer, elk and bison mainly for breeding, and all burrows were densely occupied by badgers. In pine or pine-spruce stands that are mostly rather open habitats in Naliboki Forest parent wolves made a cavity-den mainly.

Another evident trend in the wolf denning behaviour in Naliboki Forest is the increasing use of burrows to place pups during their first days, perhaps, as an attempt to save the pups from attacks of the above-mentioned inimical animals, first of all, the lynx. Before the new situation in Naliboki Forest breeding wolves mostly used open couch-dens. These dens were not so easily noticeable for the inimical animals, and

when too many mosquitos or too much smell accumulated at such a couch-den, the parent wolves easily relocated the pups in a new couch-den. Perhaps, it was also essential that not much effort was needed to prepare a new simple couch-den. Usually such couch-dens were situated in treefall. In the first decade of the 2000s and early 2010s, 72% of the wolf dens, which were found by us in Naliboki Forest (mostly without pups, recent ones, n=736 dens), were found in treefalls. Quite opposite in the new unfavourable situation for wolf denning in Naliboki Forest since 2016, about 68% of the wolf dens, which were registered by us (n= 104, again mostly without pups, recent ones), were burrows or cavity-dens.

Quite often when wolves prepare a burrow-den, they do so by enlarging the entrance of a badger sett or red fox earth. This means there are still plenty of narrow passages, made by the former owners (badgers or foxes), where the wolf pups (or at least, a part of them) may escape in the case of a lynx attack.

However, during the last 7-9 years we registered a rather fast recovery of the badger population in Naliboki Forest, in the background of the decline in raccoon dogs. The decline of the local raccoon dog population was initiated by a heavy infestation of Alaria alata helmints and scrab mange. Afterwards, the decline of the raccoon dog population was exacerbated a lot by heavy predation of lynxes and wolves. The recovered local population of badgers occupied not only all former badger setts, but also all present red fox earths, former wolf burrows and even abandoned beaver burrow networks in sandy banks of drainage canals. Interestingly, that breeding wolves, while visiting their burrow dens from the previous year, which were newly occupied by badgers, were not much aggressive towards the new owners.Perhaps, rationality of breeding wolves in this case is that it may be hard and time-consuming in the busy denning period to kill all the badgers in a given burrow to get it vacant, and, so, better to look for another den site.

Of course, such a subterrestrial den of breeding wolves helps against wild ungulate attack, but doesn't offer full protection for their pups from lynx attacks. However, for the lynx, entering such a burrow-den, it is rather risky, because the parent wolves may be nearby and attack the entering lynx. Such a lynx may be killed by them or, at least, injured severely and die afterwards from its wounds.

The last and fourth plausible adaptation of wolf breeders in the conditions of too much danger for their pups in Naliboki

(239) *Wolf father was inspecting the last year burrow-den, perhaps, to relocate the pups therein, but it was occupied by badgers, and the badger was not much afraid of the adult male wolf.*

Forest is subordination of pup-sitters that stay with the litter almost all the time. During the summer of 2018 in Naliboki Forest we documented by camera-traps the life of wolf family, which consisted of two breeding females, two different litters (10 pups altogether), the founding male and two pup-sitters. The last feature is particularly essential. One or two pup-sitters were present at pups on about 60% of the hundreds of photos taken. It looks like we have registered the features of another trend in the wolf denning behavior that we have not faced with before the lynx got common. That is when breeding wolves use pup-sitters to save their pups from the lynx or wild ungulate aggression, when they go for hunting. Interestingly, that we definitely know that these pup-sitters were non-relative wolves. Both of them were females looks like non-breeding adults.

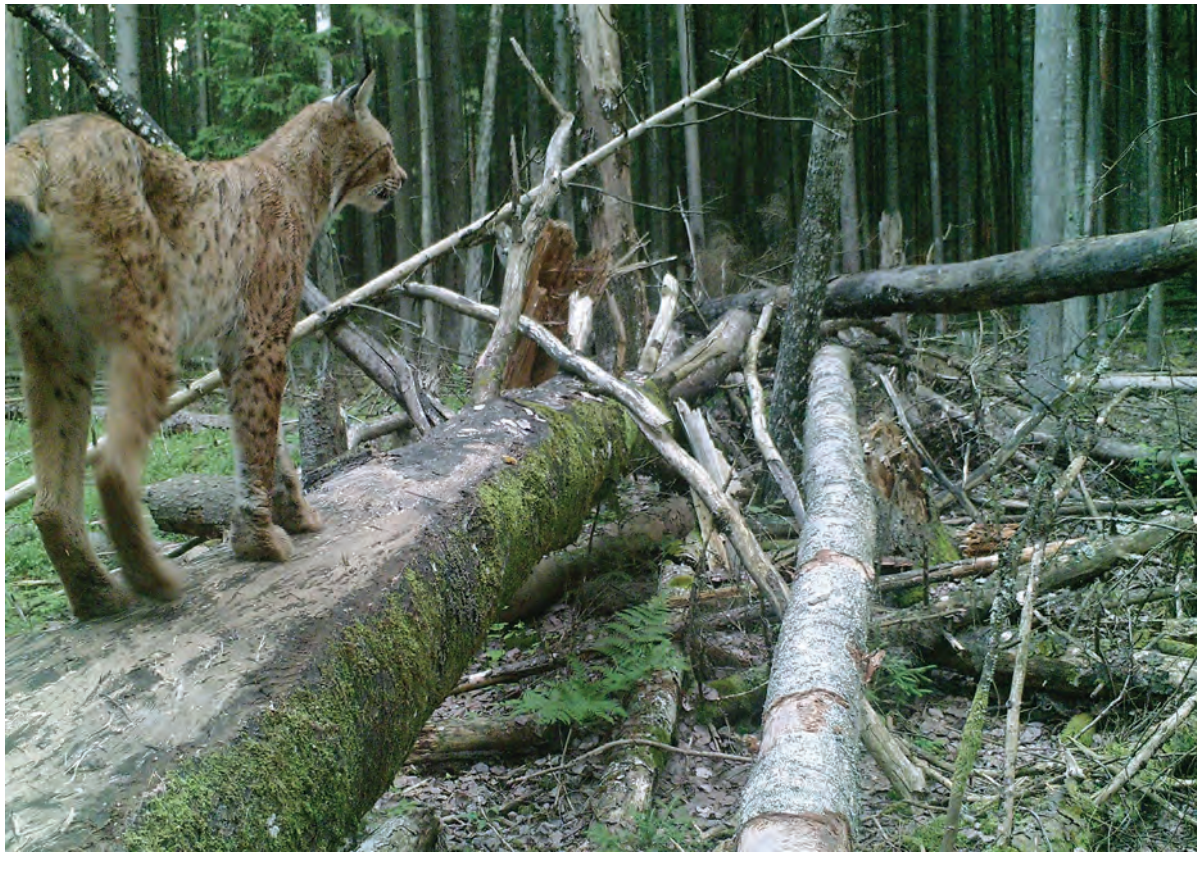
We knew that in Belarus not only the parents, but other pack members may assist to look after the pups. However, for the first time we have faced that pup-sitters spend so much time at the pups. It looks like a special non-stop guarding of pups. In the photos you may see that the pup-sitters not only guard pups, but also play a lot with them to make pups strong and smart.

(240-247) *Pup-sitters stay at the pups. They not only guard the pups more or less permanently, but also play with them quite often. Sometimes one of the two pup-sitters went for getting food for pups, in spite of the two mothers and father all the time were busy with foraging for the ten pups as well.*

(248↑) *Founding male (father) and one of the pup-sitters at the pups.*

(249↓) *One of the mothers is comming to the pups.*

(250, 251) *Adult lynx male apporoached the pup location for about 200 meters, and afterwards one of the pup-sitters checked the lynx point.*



Basic results

In Belarus, mating in wolves mostly happens within the following three social situations: (1) a mating pair only; (2) a whole pack of family origin which includes pups of the current and (or) previous biological years, with one to three females in estrus, sometimes, additionally may be one or two other adults; (3) an adult group with one to three females in estrus and one dominant male that tries to keep the breeding females for himself, whereas others males (usually one to four) keep a security distance, but tenaciously follow the mating group. If the rate of wolf persecution by humans is low or moderate, these three mating situations are more or less equally present in both protected areas and game areas. With increasing of rate of wolf persecution by hunters, or when lynxes reach moderate to high population densities, the second social situation, in which wolves reproduce (a whole pack of family origin) becomes rarer. This happens because of most of pups are killed by hunters and (or) lynxes, and wolf families are reduced up to breeders. Presence of many wild ungulates particularly bison and red deer exacerbate markedly the reproduction pitfall in wolves.

During the denning stage, a breeding unit consist of one or several pregnant females with an adult male or sometimes several males; these wolves are called 'breeders'. In most of the investigated cases, the breeders sent the rest of the pack members (mostly yearlings) away during the denning period. In this case the yearlings stayed on a distance of 3 to 8 km from the breeders for two months, at least.

Denning in wolves takes place in several denning sites (up to four) that are situated 2 to 7 km apart. In each denning site there are usually from 10 to 30 dens, between which pups are relocated by the parents. Usage of each den is short and mostly lasts up to 3 days. The choice of denning site is driven by sheltering features of habitats, presence of wild ungulates (it is better as few as possible of them), absence of lynxes (particularly an aggressive one), presence of good foraging habitats not far away and proximity of the main road in the chosen denning area. Number of mosquitos, rainy weather and human presence drive the complexity of denning behavior in wolves. Increase in these factors leads to a higher number of dens used by parent wolves.

There are four quite distinctive types of wolf dens in Belarus: pit-den, couch-den,

cavity-den and burrow-den. Normally, couch-dens are occurred more frequently. Pit-dens are used for early days pups. Burrow-dens are mostly visited by pups in the late June and till end of August. When there are too many lynxes and wild ungulates that are aggressive to wolf denning, wolves begin to use markedly more cavity-dens and burrow-dens at the early denning stage.

In Belarus, duration and importance of lactation depends on the food base. In conditions of a rich food base, milk was already not so important for pups of about 40 days old, and the mother wolves secreted only little amounts of milk. However, when prey were scarce, pups of almost 70 days old were still nursed and mothers still secreted a lot of milk. Pups had meat in their stomachs starting from the age of 20-25 days, and usually stomachs of pups of 40-60 days old rarely contained milk, but were filled with meat.

The portion of female wolves that bred was found to be irrespective of prey supply, but it markedly depended on the wolf population density. During periods of low population density of wolves 93% of adult females (in March until mid-April) were pregnant. When the wolf population density was medium, 89% of adult females were pregnant; and during periods of high population density of wolves 74% of adult females were pregnant.

Wolf pregnancy was characterized by a fairly high resorption of embryos – on average about 16%; plausibly this relates to the population density of wolves as well. During periods of low population density of wolves 8% of the embryos were resorbed; whereas when the wolf population density was medium, 20% of the embryos were resorbed; and during periods of high population density of wolves only 18% of the embryos were resorbed.

The number of non-resorbing embryos per pregnant female wolf varied from 2 to 13, and was on average from 5.0 to 8.9 in different situations in relation to the wolf population density. We did not notice any fecundity change that could be linked with the gradient of prey supply. At the same time, this fecundity parameter had markedly higher values, when the population density of wolves was low.

Heavily pregnant female wolves are not rarely killed by lynxes; approximately one per 20 such females is killed by lynxes, when the lynx population density is higher than 2 inds per 100 km².

The size of wolf litters up to 20 days old varied from 2 to 10 pups, on average 6.1. There was a marked between-year varia-

tion in the mean litter size from 4.8 to 7.7 pups. Litter size was significantly negatively correlated to the wolf population density. The inversely density-dependent increase in litter size concerned only female pups. The average number of females in a litter varied from 2 at the highest population density to 5.4 at the lowest population density. The number of male pups in a litter was not related to wolf population density and averaged 2.8. A similar trend was revealed in relation to the sex-ratio in wolf pups; the lower the wolf density, the bigger the proportion of females amongst pups was recorded.

We found that multiple breeding in a wolf pack is a common phenomenon in Belarus. By investigating in details denning situation in 59 wolf breeding groups across longer than twenty years (until 2019) in Naliboki Forest and Paazierre Forest and having 74 dens with pups found, we revealed 17 cases of double breeding and 2 cases of triple breeding in a wolf pack. So, multiple breeding in wolf pack happened, at least, in 32% of denning cases. By performing necropsies on wolf carcasses, we found multiple breeding to occur in about 22% of breeding cases. The main reason for multiple breeding was mating of the dominant or founding male (perhaps the father) not only with the founding female (mother), but also with subdominant females (mainly daughters). Taking into account that not in all cases of wolf denning the possibility of multiple breeding was checked sufficiently (*i.e.* when other possible litters could be not discovered), we assume that actually multiple breeding in wolf packs occurs even more often than can be derived from our data.

Multiple breeding in a wolf pack was registered as not a short-term phenomenon in a single local population of the species, but during two decades in two different large forest massifs.

In Belarus the phenomenon of multiple breeding in a wolf pack is evidently connected with the low density of the whole wolf population, and seems to occur irrespective of the food base. We consider multiple breeding in wolf packs as a population reaction on the unsaturated state of the population and the relatively low density, in order to increase the reproduction and compensate the loss (mainly from human persecution). In other words, it is a density-dependent regulation of reproduction.

We registered three cases of breeding of yearling females. The data suggests that approximately 5-8% of yearling females in the wolf population already breed in Belarus. This peculiarity may be considered as the response of the wolf popula-

tion to intensify the reproduction in the conditions of excessive elimination of wolves by hunters mainly.

Among seven well-documented cases of hybridization between wolves and stray dogs, three cases were registered in Naliboki Forest, when the wolf population was quite dense. Nonetheless, hybridisation in conditions of low population density in wolves may also be interpreted as an action triggered by the low population density and an attempt to recover the rarefied wolf population. Interestingly, in all seven cases of wolf-dog hybrid breeding, only female stray dogs (naturalized ones) and male wolves created a hybrid family.

Timing of parturition in the wolf population is seemingly getting more prolonged, or there are just many exceptions. In the 2000's, among 65 parturitions, which were well-documented, we registered one parturition in mid-January, four parturitions in late March-early April and four parturitions in the last ten days of May. The majority of the registered parturitions in wolves were dated within a normal seasonal period, *i.e.* the last ten days of April until mid May.

In Belarus, the survival in wolf pups was found to be low or very low. The causes of wolf pup mortality were the following. First of all, parents deliberately leave some pups to die, when they relocate young pups from one den to another. This particularly happens, if the litter is large (8-12 pups). Therefore, we registered significantly higher mortality in larger wolf litters. When the food base gets too poor, even older pups may be abandoned by their parents.

Killing by lynxes and wild ungulates are other common causes of mortality of wolf pups. It looks like, at least, a half of the wolf pups are killed by lynxes in the habitats, where the lynx population density is 2 inds per 100 km² and higher. As to wild ungulates, our data suggests that killing of wolf pups by wild ungulates usually constitutes up to 10% of overall pup mortality by the first winter. However, if wild ungulates are spread widely in the whole variety of available habitats and their population density is high (15-20 and more inds per km², except roe deer), up to a quarter of the present wolf pups may be killed by wild ungulates during the first three months of pups. We think that mainly bison, stags (adult male red deer) and both sexes of adult elks may be responsible for this high percentage of ungulate-caused mortality.

By tracing 33 wolf litters from birth (mostly in the first half of May) till the beginning of winter (November-December) in Paazierre Forest, we found that the survivalship in wolf pups was rather low –

0.48 on average (*i.e.* 52% of pups died during the first 6-7 months).

As to mortality of wolf pups in Naliboki Forest, we separated our data for three periods characterised by different states and densities of the local lynx population. We calculated that in 1999-2011, with a low number of lynxes, the mortality in wolf pups was about 30%; in 2012-2016 with markedly more lynxes the mortality in wolf pups was 63%; in 2016-2017, when lynxes reached relatively high densities, an extremely high mortality (96%) in wolf pups was registered.

Ambient factors influence survivalship of wolf pups. Placing of wolf pups in burrows by their parents leads to a higher survival rate in pups before winter. Long distance relocation of pups leads to a lower survivalship of them. Rainy weather leads to more complicated denning behavior (more denning sites, more dens in each site and longer distance of relocation between the denning sites), which in turn leads to a lower survivalship. Conversely, during more or less dry weather more complicated denning behavior leads to a higher survival rate. Along with the weather, the number of mosquitos and human presence drive the complexity of denning behavior and may increase the mortality in pups indirectly.

The gained data on wolf pup mortality suggest the crucial role of lynx predation for the survival of wolf pups. It is becoming evident that, when in a forest massif the lynx reaches a high population density, the local wolf population appears in a "trap" due to a reproduction "pitfall". The reproduction problems in wolves are based not only on interference of lynxes towards wolves at breeding, but also on the manner of wolves to raise pups. This manner of wolf breeders is leaving pups alone for quite long in a sheltered site, when parents go foraging.

When lynxes cause problems for the reproduction of wolves in a forest massif, the local wolf population becomes persisting not due to reproduction, but because of immigration of wolves from adjacent rural-forest mosaic terrains, where pups survive easier with few or no lynxes in the habitats. Again, presence of many wild ungulates particularly bison and red deer stags exacerbate markedly the problems of reproduction in wolves.

Wolves were not always in such a critical situation. Two to three centuries ago lynxes as well as wild ungulates were not so common in the vast Belarussian forests, which contained a lot of undisturbed areas. In recent times, intensifying of logging with early reforestation on clearcuts condi-

tioned markedly higher habitat carrying capacity for wild ungulates and lynxes. Lynx numbers increased manifold, and frequency of wolf-lynx interference increased a lot. We hypothesize that just logging is responsible for the increase in lynx numbers that, in turn, leads to the reproduction "pitfall' in wolves that inhabit forest massifs.

Peculiarities in the formation of wolf packs were frequently found. Offspring often stayed with their parents for three to five years without breeding instead of normal two years.

At the same time, we noticed an opposite trend of absence pups in wolf packs that is evidently connected with pack deterioration through wolf persecution by humans or/and because of extremely low survival of pups. Both situations lead to pack formation with non-relatives sometime during autumn, when strong wolves gradually subordinate other non-relative wolves that are ranging around. In such situations the majority of wolf packs in winter mostly consisted of non-relative individuals. For instance, in 2015-2019 in Naliboki Forest, when lynxes reached a fairly high density and killed most of the wolf pups, the majority of wolf packs were entirely or mainly of non-family origin, *i.e.* mainly consisted of non-relative, subordinated individuals.

During 2015-2019 in Naliboki Forest, when lynxes got common, and the reproduction in the local wolf population nearly stopped, the wolf population still existed due to the immigration of adult wolves during mating season, while in 2000-2012 the local wolf population in Naliboki Forest existed because of its intensive reproduction.

In the conditions of too high density of lynxes and wild ungulates (particularly bison and red deer), wolf breeders change a lot their denning behaviour, trying to save their pups. They move from denning-inimical habitats outside of forest massif. Also, wolf breeders begin to use markedly more closed dens as a cavity-den and a burrow-den. They switch denning for pine or pine-spruce stands with poor forest floors, where lynxes and wild ungulates are present rarer in the wolf denning season. Also, wolf breeders locate more frequently pups in open grasslands, whereas lynxes avoid this habitat type. To save pups, wolf parents may subordinate other non-breeding wolves for pup-sitting. Such a pup-sitter may be even non-relative.

Literature:

Ballard W.B., Whitman J.S., & Gardner C.I. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildlife Monographs, no.98. The Wildlife Society, Bethesda, MD.

Bergmanis U., Ķuze, J., Lipsbergs, J., Hofmanis H. 2012. Distribution, population dynamic, ecology and protection of Golden Eagle Aquila chrysaetos in Latvia // Kungsörnen 2012, 52-60.

Bibikov D.I. 1985. The Wolf. History, Systematics, Morphology, Ecology. Nauka Publisher, Moscow. [In Russian]

Danilov P.I., Gursky I.G. & Kudaktin A.N. 1985. Reproduction. – In: Bibikov D.I. 1985. The Wolf. History, Systematics, Morphology, Ecology. Nauka Publisher, Moscow: 378-389. [In Russian]

Debrot S., Fivaz G., Mermod C. & Weber, J.M. 1982. Atlas des poils de mammiferes d'Europe. Ed. Inst. Zool., Univ. Neuchatel, Neuchatel.

Gibson P.S., Ballard W.B., Nowak R.M. & Mech L. 2000. Accuracy and precision of estimating age of gray wolves by tooth wear. Journal of Wildlife Management 64: 752-758.

Jędrzejewska B., Jędrzejewski W., Bunevich A.N., Miikowski L. & Okarma H. 1996. Population dynamics of wolves Canis lupus in Białowieża Primeval Forest (Poland and Belarus) in relation to hunting by humans, 1847-1993. Mammal Review 26:103-126.

Jędrzejewska B. & Jędrzejewski W. 1998. Predation in Vertebrate Communities. The Białowieża Primeral Forest as a Case Study. Springer Verlag, Berlin.

Jędrzejewski W., Jędrzejewska B., Okarma H., Schmidt K., Zub K. & Musiani M. 2000. Prey selection and predation by wolves in Białowieża Primeval Forest, Poland. Journal of Mammology 81(1): 197-212.

Jędrzejewski W., Schmidt K., Theuerkauf J., Jędrzejewska B.& Okarma H. 2001. Daily movements and territory use by radio-collared wolves (*Canis lupus*) in Białowieża Primeval Forest in Poland. Canadian Journal of Zoology 79: 1993-2004.

Jędrzejewski W., Schmidt K., Theuerkauf J., Jędrzejewska B., Selva N., Zub K., Szymura L. 2002. Kill rates and predation by wolves on ungulate populations in Białowieża Primeval Forest (Poland). Ecology 83(5): 1341-1356.

Jędrzejewski W., Schmidt K., Theuerkauf J., Jędrzejewska B., Kowalczyk R. 2007. Territory size of wolves Canis lupus: linking local (Białowieża Primeval Forest, Poland) and Halarctic-scale patterns. Ecography 30: 66-76.

Jędrzejewski W, Jędrzejewska B, Andersone-Lilley Z, Balciauskas L, Mannil P, Ozolins J *et al.* (2010). Synthesizing wolf ecology and management in Eastern Europe: Similarities and contrasts with North America. In: Musiani M, Boitani L, Paquet PC (eds). The World of Wolves. New perspectives on Ecology, Behavior and Management. University of Calgary Press: Calgary, 207–233.

Klevezal G.A. 1996. Recording structures of mammals. Determination of age and reconstruction of life history. Balkema Publishers, the Netherlands, Rotterdam.

Kreeger T.J. 2003. The internal wolf: physiology, pathology, and pharmacology. In: Mech, L. David; Boitani, Luigi, eds. (2003). Wolves: Behaviour, Ecology and Conservation. University of Chicago Press: 192-217.

Likert R. A. 1932. Technique for the Measurement of AttitudesArchives of Psychologytechnique for the measurement of attitudes, Arch. Psychol. 140: 1–55.

Mech L.D. 1975. Disproportionate sex ratios of wolf pups. Journal of Wildlife Management, 39: 737-740.

Mech L. D. 1988. The Arctic Wolf.Voyageur Press

Mech L.D., Adams L.G., Meier T.J., Burch J.W. & Dale B.W. 1998. The wolves of Denali. University of Minnesota Press.Minnepolis.

Mech L. D., Boitani L. eds. 2003. Wolves: Behaviour, Ecology and Conservation. University of Chicago Press.

Mech L. D., Barber-Meyer Sh. M. & Erb J. 2016. Wolf (*Canis lupus*) Generation Time and

Proportion of Current Breeding Females by Age. PLOS ONE 11(6): e0156682. doi:10.1371.

Paquet, P. & Carbyn, L. W. 2003. Gray wolf *Canis lupus* and allies", in Feldhamer, George A. et al. Wild Mammals of North America: Biology, Management, and Conservation, JHU Press: 482-510.

Stronen A.V., Jedrzejewska B., Pertoldi C., Demontis D., Randi E., Niedzialkowska M., Pilot M., Sidorovich V.E., Dykyy I., Kusak J., Tsingarska E., Kojola I., Karamandilis A.A., Ornicans A., Lobkov V.A., Dumenko V., Czarnomska S.D. North-south differentiation and region of high diversity in European wolves (Canis lupus) PLOS ONE, October 2013. Vol. 8. Iss. 10, e76454. (IF 3.73)

Sidorovich V.E. 2011. Analysis of vertebrate predator-prey community. Studies within the European Forest zone in terrains with transitional mixed forest in Belarus. Tesey, Minsk.

Sidorovich V.E. & Vorobej N.N. 2013. Mammal activity signs: Atlas, identification keys and research methods. Skills gained in Belarus. Veche, Moscow.

Sidorovich V.E. 2016. Naliboki Forest: Land, Wildlife and Human. Minsk, Chatyry Chverci.

Sidorovich V. & Rotenko I. 2014. Abnormal features of the wolf population in Belarus: pack multi-breeding, breeding of yearling females and hybridization with stray dogs. Is this an influence of the rich prey supply or low density of the wolf population that affected by human persecution? – In the abstract of the conference: "European large carnivores: problems of small-sized populations, study on reproduction, and challenges of reintroduction programs". Minsk, NiktagraphicsPlus, 2014. P.:37-38.

Sidorovich V., Schnitzler A., Schnitzler Ch., Rotenko I., 2017. Wolf denning behaviour in response to external disturbances and implications for pup survival, Mammalian Biology – Mammalian Biology 83: 1-7.

Sokal R.R. & Rohlf F.J. 1995. Biometry: the principles and practice of statistics in biological research. W. H. Freeman and Company, New York.Teerink B.J. 1991. Hair of West-European Mammals. Cambridge University Press, Cambridge.

Stronen A.V., Jedrzejewska B., Pertoldi C., Demontis D., Randi E., Niedzialkowska M., Pilot M., Sidorovich V.E., Dykyy I., Kusak J., Tsingarska E., Kojola I., Karamandilis A.A., Ornicans A., Lobkov V.A., Dumenko V., Czarnomska S.D. North-south differentiation and region of high diversity in European wolves (*Canis lupus*) PLOS ONE, October 2013. Vol. 8. Iss. 10, e76454. (IF 3.73)

Theuerkauf J., Rouys S. & Jędrzejewski W. 2003. Selection ofden, rendezvous, and resting sitesby wolves in the Białowieża Forest, Poland. Can. J. Zool. 81:163-167.

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НДАБ. Ф. 694. В. 3. С. 1229.

НДАБ. Ф. 1363. В. 1. С. 2677. А. 60-62

Niemcewicz J.U. 1868. Pamietniki czasow moich. Lipsk.Успаміны Крыштафа Завішы ваяводы мінскага (1966-1721). 2011. - Выданне з арыгінальнага рукапісу з заўвагамі Юльяна Барташэвіча ў перакладзе з польскага Віктара Хурсіка. Мінск. Выдавецтва В. Хурсіка.

Шышыгіна-Патоцкая К.Я. (Shyshyhina-Patotskaya). 2007. Нясвіж і Радзівілы. Мінск, Беларусь.

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