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Wolves impact on the moose population

Key words: *Canis lupus*, *Alces alces*, specific survival rate, absolute number of killed prey

1. Introduction

An enormous number of both theoretical and experimental works is devoted to relations in the “resource-consumer” and “predator-prey” systems, including particular studies of “moose-wolf” relationships. Suffice to mention the studies performed on the island of Isle Royale.

There is extensive literature on the diet of wolf. Also there is plenty of studies on the ungulates’ mortality, based on the findings of their remains. Besides there are publications which analyze predator/prey abundance ratio and basing on these data conclude about the relative role of a predation on different phases of prey population dynamics. Other works show clear selectivity in consumption of young and old animals. Finally, there are theoretical models, according to which the predator can not exert an overwhelming influence on the abundance of the prey species. None of these lines of research has given a correct answer regarding the actual quantitative effect of wolves’ predation on prey population as a whole.

Estimates of the absolute mortality of ungulates, particularly moose, resulting from predation by wolves and other causes, except legal hunting, is the missing link in all studies of relationships in the system “large carnivores – ungulates”. Lack of such estimates does not allow to combine different fields of research in this area.

We attempted to obtain such an estimate, using a special method for assessing the losses from predation, allowing to determine absolute and specific losses from both carnivores and illegal hunting. Index of absolute mortality was obtained by comparing the specific survival (mortality) of animals with the distribution of the relative mortality from different factors (obtained from the questionnaire survey of game management personnel and hunters), population size and growth rate of carnivores and ungulates.

Estimate of the specific survival rate was obtained by compiling life tables (CAUGHLEY 1979) based on data on the rate of population growth, fertility, and the absolute age of the legally hunted animals

Moose is a large animal and thus, after finding the remains of dead individuals, researchers have a unique opportunity to determine, with the certain degree of accuracy, the cause of death. There is a number of studies on assessing the structure and relative magnitude of mortality of moose (PEROVSKI 1988, 2003; GLUSHKOV, PIMINOV, PONOMAREV 1989, FILONOV & KALETSKAYA 1982; FILONOV 1989; GORDIYUK 1980; VERESHCHAGIN & RUSAKOV 1979, TROITSKII 1974; KHERUVIMOV, 1969; ZHIRNOV & METELSKY 1965; LIKHACHEV 1965; GLUSHKOV 1988; BAIDAVLETOV 1989, and others, see review in DANILKIN, 1999). Most studies show that the main reasons of the death of ungulates are poaching and pre-

dation. Studies based on the analysis of large datasets (PEROVSKI 1988; GLUSHKOV, PIMINOV, PONOMAREV 1989) demonstrated that in the Russian Federation in 1980-s the average contribution of these factors in the mortality of moose was approximately 30% of the total mortality excluding that related to legal hunting. In recent years the level of poaching in many regions of Russia has grown significantly, both in hunting grounds and in protected areas. Following N.M. GORDIYUK (2002), in the Bashkirsky Nature reserve the relative mortality of moose from poaching is 56.5 %, while from all the predators – 20,3 %, and the wolf – only 11,6 % of the total mortality.

Predation by wolves, lynx and feral dogs is characterized by pronounced selectivity. The nature of selectivity varies depending on the prey species – among moose, killed by wolves, the increased proportion of yearlings has been reported (FULLER & KEITH 1980; PETERSON, 1984), and the same concerns the proportion of females among adults (SOBANSKY 1976; PETERSON et al. 1984), although there the opposite view (see FULLER & KEITH 1980).

Analyzing these data we can determine the power of different factors of mortality, identify main and secondary factors. But based on these data, we, of course, cannot say, how many moose (in absolute terms) die from the different reasons. Knowledge of the size of moose mortality in absolute terms, will help solving many issues, which are currently unclear, in particular, we'll be able to determine the effect of illegal hunting, the losses of moose from predation by wolves, etc.

2. Material and Methods

The structure of mortality was analyzed basing on the results of the interrogation survey performed among hunters and game management personnel in cooperation with The Department of Game Management of Sverdlovsk region in 1998–2003 (KORYTIN, MARKOV, POGODIN, 2007).

The questionnaires recorded cases of detection of dead animals. The finder, if possible, determined the cause of death, sex and approximate age of the dead animal. Questionnaire material

may contain a significant amount of both random and systematic errors, which strongly can affect the result in case of a small sample size. The authors are aware of it, however, in modern conditions other alternative ways of gathering this material is impossible.

The authors also used data on 687 moose, harvested by hunters in the seasons 1988/1989, 1995/1996 and 1996/97 for which was determined the age by counts of of the incisor cement layered structures (KLEVEZAL & KLEINENBERG 1967).

Information about each animal included date and place of kill, sex and the number of embryos. The volume of data was obtained by collecting from the hunters parts of the lower jaws of killed moose and also questionnaires containing detailed information about harvested animals. Life tables were prepared by standard methods described in CAUGHLEY (1979).

Calculation of the absolute mortality of moose on different factors was done using a specially developed technique.

3. Results and discussion

Specific survival rates of moose were calculated for the seasons 1988/89, 1995/96 and were respectively 0.757 and 0.714 (average for males and females together, Tables 1, 2).

Accordingly, the specific mortality rates were 0.243 and 0.286. The growth rate, assessed after taking into account differences in the fecundity of females of different age, was 14,5 % in 1988, and 26,7 % in 1995. Distribution of mortality from various factors (except legal hunting) was obtained by analyzing the 1456 registered deaths of ungulates during the period from 1998 to 2002. Analysis of 581 cases of deaths of moose gives the following picture of the contribution of different factors to mortality:

- killed by poachers - 53 %;
- killed by wolf - 18,8 %;
- killed by brown bear - 2,6 %;
- killed by unknown predator - 4,6 %;
- died as a result of injuries - 3,6 %;
- died as a result of wound - 4,0 %
- drowned - 2,4 %;
- starvation - 2,2 %;
- cause of death is not defined - 8,8 %.

As could be seen from the tables, the most powerful factor in non-hunting mortality is poaching (53 %), the contribution of wolf, the main predator, is of 18,8 %.

The contribution of wolf to the mortality of moose in different regions of Sverdlovsk region is not related to the average density of moose, but to some extent, it is directly proportional to the population density of wolf ($R^2 = 0,31$).

The contribution of wolves to moose' mortality in different parts of Sverdlovsk region is most strongly related to the moose/wolf abundance ratio ($R^2 = 0,45$; $r = 0,67$).

The smaller is the number of moose per one wolf, the higher is the contribution of wolf in moose mortality. Thus, the greater is the impact of wolves on moose populations.

For instance, in the northeastern part of Sverdlovsk region wolf density is 0.037 ind/1000 ha, the ratio of moose / wolf is minimal and is equal to 35.5, while the contribution of wolf in moose mortality is the highest and equals 28 %.

In the southeastern part of Sverdlovsk region the population density of the wolf is twice lower (0.016 ind./1000 ha), the ratio of moose / wolf is 108.2, and the percentage of wolf in moose mortality is 14,5 %.

As could be seen from *Table 3* in the season 1988/89. when the total number of moose was about 21 thousand individuals, poachers killed 1540 moose, while in the season 1995/96. when the total population was of 19,5 thousand individuals, poachers have killed 3,350 animals, thus more than twice as much.

Note that losses from wolves' predation are three times lower than those from illegal hunting. Thus, as a result of predation by wolves losses equaled 2–5 % of spring population of moose, and one wolf killed about one elk per year. After 50 % decrease in the "moose / wolf" abundance ratio, the specific harvest of wolf increased by only 21 %. These results suggest that even when the ratio of moose / wolf abundances is 20:1 the wolf can not exert an overwhelming

Table 1 Estimates of specific survival of moose for adjusted for growth rate age distribution in the season 1988/89.

Age class	Males			Females		
	1	2	3	1	2	3
0+	132	132		108	108	
1+	123	123		102	102	
2+	119	125,57	0,86	95	100,25	0,9
3+	97	108,01	0,816	81	90,2	0,924
4+	75	88,13	0,802	71	83,43	0,918
5+	57	76,58	0,796	57	76,59	0,944
6+	43	62,2	0,785	50	72,33	0,818
7+	32	49,84	0,89	38	59,18	0,765
8+	27	45,27	0,964	27	45,27	0,638
9+	21	37,91	0,718	16	28,88	0,606
10+	14	27,21	0,615	9	17,49	0,837
11+	8	16,74	0,942	7	14,65	0,769
12+	7	15,77	0,615	5	11,27	0,861
13+	4	9,70	0,538	4	9,7	1,077
14+	2	5,22	0,538	4	10,45	0,538
15+	1	2,81		2	5,62	0,538
16+				1	3,03	
average 2+-16+			0,747			0,779

Fig. 1 The population dynamics of moose and wolf, and the ratio of moose/wolf populations in the Sverdlovsk region; 1 – the number of moose (divided by 10), the left vertical axis; 2 – moose/wolf abundance ratio, right vertical axis; 3 – the number of wolves, the left y-axis

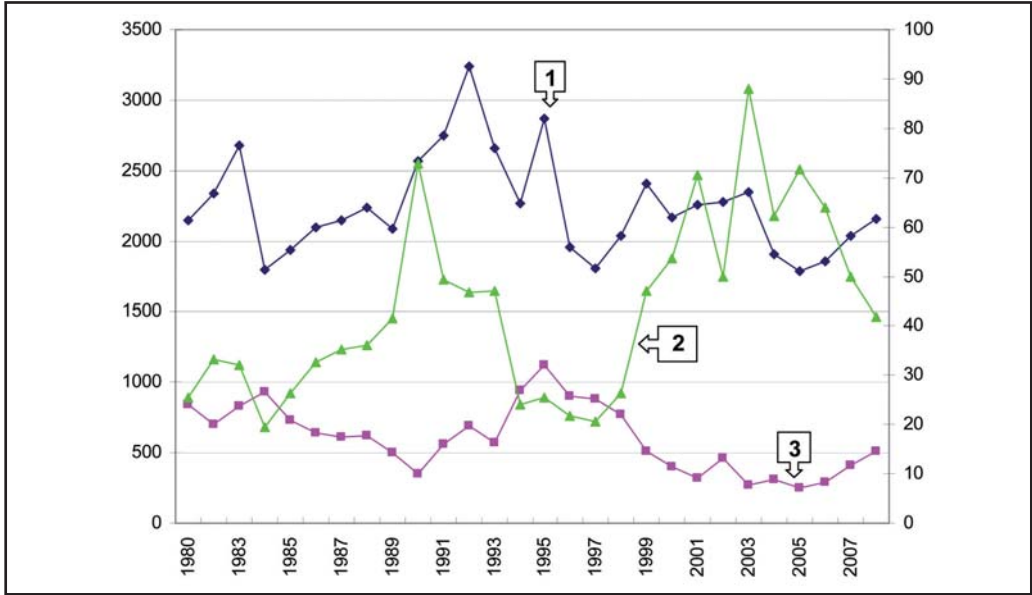


Table 2 Estimates of specific survival of moose for adjusted for growth rate age distribution in the season 1995/96

Age class	Males			Females		
	1	2	3	1	2	3
0+	115	115	0,946	90	90	0,924
1+	106	108,81	0,688	81	83,15	0,849
2+	71	74,82	0,839	67	70,60	0,781
3+	58	62,74	0,814	51	55,17	0,725
4+	46	51,08	0,714	36	39,97	0,798
5+	32	36,48	0,738	28	31,92	0,770
6+	23	26,91	0,803	21	24,57	0,684
7+	18	21,62	0,741	14	16,82	0,660
8+	13	16,03	0,632	9	11,10	0,684
9+	8	10,13	0,642	6	7,59	0,684
10+	5	6,50	0,205	4	5,20	0,513
11+	1	1,33	1,027	2	2,67	1,027
12+	1	1,37	1,027	2	2,74	0
13+	1	1,41				
average 2+- 13+			0,696			0,733

1 – number of animals in the age class; 2 – number of animals in the age class adjusted for the growth rate;
3 – specific survival rate.

influence on the number of moose. Information from the literature on the distribution of the deaths of moose from different reasons (based on found remains) indicate that in the nature reserves, where poaching is not an explicit factor of mortality (at least theoretically), the relative contribution of wolf (in the absence of other big prey) can increase to 85 % of mortality (based on publications by K. FILONOV). Rough calculations made for this case give an estimate of the specific mortality from wolf that is equal to approximately 3-4 moose per year.

Note that the main factor of mortality in the population of moose in the Sverdlovsk region in 1990-ies is poaching, and, apparently, the level of poaching has continued to grow. Our estimates of specific survival for a hunting season 1996/97 was even lower and for males it was equal to the value of 0.58. The level of legal hunting and the number of wolves decreased, hence the level of poaching should be even higher than in the season 1995/96. Our estimate of the proportion of moose harvested by wolf – 2–5 % – is consistent with direct observations of the wolves' hunting success on the Isle Royale. In one case it was equal to 4,6 % (MECH 1970), in the other case – 2 % (PETERSON 1977). Annual wolf's demand for food was estimated based on the weight of stomach contents as approximately 500–800 kg (The Wolf, 1985). Estimates of proportion of moose in the diet of

the wolves varies considerably in the publications by various authors, and also depends from the region. Approximately it can be estimated at 30–50 % on average. Given that the average weight of moose carcass is about 200–250 kg, our estimate of the rate of consumption in 1–1.2 elk per year (2–5 % of the total elk population) is consistent with earlier studies done by other authors.

Figure 1 shows the change in the number of moose and wolves in the Sverdlovsk region and the ratio of moose / wolf population densities. As could be seen from the graph, the population of wolf slightly lags behind changes in the number of moose. The first peak of moose abundance was observed in 1983, and the peak of the number of wolves – in 1984, next peak of moose population occurred in 1992, and the peak of the number of wolves – in 1995. This delay suggests that the wolves' population dynamics follows changes in abundance of moose, but not vice versa. In other words, the wolf has no significant effect on the number of moose. On the other hand, the moose-wolf ratio was minimal (at 20:1) exactly in the periods of depression of moose population.

Decrease of moose populations in the early and mid 1990's occurred throughout the vast territory of Russia. The demographic analysis, performed by us, showed that, at least in the Sverdlovsk region a decline in moose popula-

Table 3 Comparison of the main population parameters and indexes of the absolute mortality of moose in the seasons 1988/89 u 1995/96

Parameter	Season 1988/89	Season 1995/96
Population size, ind.	21000	19600
<i>Specific survival *</i>	<i>0,76</i>	<i>0,71</i>
<i>Growth rate, %</i>	<i>14,5</i>	<i>26,7</i>
Legal hunting bag, ind.	2848	1266
Wolves' population, ind.	500	900
<i>Total number of moose killed by wolves, ind.</i>	<i>472</i>	<i>1027</i>
<i>Specific harvest of moose per wolf, ind.</i>	<i>0,94</i>	<i>1,14</i>
<i>Ratio of moose/wolf abundance, ind.</i>	<i>41,6</i>	<i>21,8</i>
<i>Number of moose killed by poachers, ind.</i>	<i>1540</i>	<i>3350</i>
<i>Number of moose killed by poachers per one legally hunted, ind.</i>	<i>0,54</i>	<i>2,65</i>
* - parameters in italics indicate calculated indexes.		

tion is not a result of decrease in fertility, but it resulted from the increase in mortality, which in turn occurred largely as a result of growth in the trivial poaching, rather than increased predation by wolves. Although the smallest ratio of moose and a wolf is typical for periods of recession the number of moose.

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Summary

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The original calculative method of the absolute moose mortality was specially designed for measuring the direct wolf impact on the moose population. The specific survival rate of animals was the basis of methodology. Amount of the moose population losses from wolf predation constitute 2–5 % of the total number, one wolf consume 0.9–1.2 moose per year an average. Significant wolf impact on moose population may occur when the ratio of “moose: wolf” become 20:1 or less.

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