FACTORS DETERMINING MOOSE POPULATION DYNAMICS IN THE CENTRAL FOREST RESERVE

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ABSTRACT: We determined the main factors that led to a decrease in the moose population of the Central Biosphere Reserve. The role and importance of the factors in this process were defined. The key role of predation by wolf in the moose population decline is emphasized. The predominant factor leading to the decrease in the moose population was wolf predation, which exerted a pronounced effect on the moose population number and on its age and sex composition.

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Review of the literature on ungulate–forest interactions shows some conflicting opinions that will require further detailed study. Nevertheless, there are data that allow estimation of the role of this group of animals in natural ecosystems. The appraisal of moose–forest interaction is complex and, to a certain degree, contradictory due to differing points of view of authors with respect to the forest as a whole and to moose in particular (Filonov 1983). Moose damage plant cover and thus cause changes not only in the structure and productivity of brush and woodland vegetation but also in the composition of leaf litter and properties of soils (Pastor et al. 1988). The extent of influence by moose on vegetation depends on moose population density (Gatikh 1980) and determines the characteristics of changes in natural forests. This is especially important for the ecology of reserves.

STUDY AREA

Observations were performed in a 1,000 km^2 area in the Central Forest Biosphere Reserve, including a wildlife protection area and a sporting zone.

METHODS

The data described below were obtained during 1975–1985 in the Central Forest Reserve. Several points were confirmed by data of the Tver State Hunting Inspectorate. We also used the reserve's archives. Causes of moose deaths were assigned to one of four categories: (1) wolf predation; (2) brown bear predation; (3) illegal human hunting; and (4) drowning. Changes in the composition of the moose population by sex and age caused by wolf predation and human harvest in the study area were estimated on the basis of inspection of wolf–killed prey and human harvest.

RESULTS AND DISCUSSION

During the study period the moose population decreased from 340/1,000 km^2 in 1975 to 66–80/1,000 km^2 during 1980–1985. The archives and questioning of inhabitants revealed that the moose number in the study area also fluctuated before this period. Moose density during 1917–1919 was 180/1,000 km^2 in this area. At that time the moose density for the adjacent territories was 300/1,000 km^2. Due to hunting, the moose population declined and during 1931–1932 there were only 2 moose in the reserve. The population density started to increase again from 44/1,000 km^2 in the winter 1940–1941 to 231/1,000 km^2 in 1949–1950 (Yurgenson and Yurgenson 1951). The highest moose populations were during 1957–1962; however, a decrease occurred, followed by another increase from the late 1960s to the early 1970s. The population number started to decline again in 1977 (the density in the reserve was 320/1,000 km^2 and 274/1,000 km^2 in the protection area). In 1978 the density was 280/1,000 km^2 in the reserve and 230/1,000 km^2 in the protection area, and in 1979 the density was down to 120/1,000 km^2 in both the reserve and the protection area.

Thus, the population dynamics in the territory of the reserve are characterized by increases and decreases of moose numbers and by periods of stabilization at both high and low density. Lower moose densities from 1919 to 1931 reflected losses mainly due to anthropogenic factors; from 1977 to 1983 other influences should be taken into account. Density reduction was observed everywhere in the Tver region. In 1976, 1977, 1978, 1984, and 1985 the moose population numbers were 17,616, 18,080, 19,548, 12,000, and 7,000, respectively (the first 3 values were derived from winter migration observations and the others from aircraft–assisted observations). A decrease in population was observed in most parts of the Tver region. In the Toropetskii district there were 968 moose in 1971 yet only 382 moose in 1983; at the same time the population decreased 2–fold in the Selizharovskii district and 3–fold in the Lesnoi district.

Direct observations and tracking analysis in the territory of the reserve revealed that during June through August (n = 441), on average, there was 0.93 calves per cow and 0% twins in 1965, 0.40 and 0% in 1970, 1.00 and 50% in 1973, 1.00 and 47% in 1974, 0.75 and 33% in 1975, 1.50 and 33% in 1977, 0.90 and 33% in 1978, 1.13 and 47% in 1979, 1.00 and 0% in 1980, 1.00 and 0% in 1981, and 0.75 and 33% in 1982. Mean values for cow moose embryo counts and twinning rates in the Tver region during 1977–1979, based on the results of licenced hunting, were that the embryo number was 1.32 per cow with calf and 0.78 per mature cow, with a 32% occurrence of twins. In the Yaroslavl region the mean values of these parameters during the same period were very close to those mentioned above. In the Moscow region, the percentage of twins increased from 16% in 1977 up to 43% in 1980, and the embryo number per cow with calf increased from 1.16 to 1.43 (Filonov 1983). We can conclude that moose productivity in the reserve did not decline during 1977–1970, and the decrease in population number was therefore due to some other cause.

There were no changes in climate that deviated from normal mean values during the long–term observations. Human factors (both direct and indirect influences) were not significant. On average, no more than 10–12 moose were harvested per year (only 2.5–3.0% of the population at the beginning of the biological year). The natural increase of the population was 16.3% in 1975 and 16.4% in 1976. Hence, anthropogenic factors could not play a crucial role in the decline of the moose population. During the period under study, abiotic factors did not differ greatly from the mean values for many years. No mass moose migrations were observed. If the factors mentioned above cannot explain the population fluctuations, it is reasonable to consider the role of predators.

Causes of moose deaths (n = 71) were assigned to one of four categories: (1) wolf predation (79%); (2) brown bear predation (19%); (3) illegal human hunting (1%); and (4) drowning (1%). It was assumed that during 1975–1977 in the study area, the bear harvest was 3–5% and wolf harvest

21% of the population. The number of wolf–killed moose was greater than the natural rate of population increase; thus, wolves crucially affected the moose population.

This assumption is corroborated by the fact that in spite of the total decline of the moose population, several areas were characterized by an increase in moose numbers, depending on the pressure of wolves on moose. In the Vesyegonskii district the moose population number increased from 825 in 1977 to 830 in 1979, 1,050 in 1981, and 1,105 in 1983. This increase was promoted by a low predator population number; from 1976 to 1982 the wolf density was 5.4–9.3 per 1,000 km^2 (the average density in the entire Tver region was 16–22 per 1,000 km^2) and the wolf–to–moose ratio was in the range of 1:75–1:58. In the Kashinskii district the moose number was 256 in 1976 and 700 from 1981 to 1983; the wolf density was 2–7 per 1,000 km^2 from 1978 to 1983 (there were no wolves registered in the district during 1976–1977) and the wolf–to–moose ratio varied from 1:64 to 1:50.

Changes in the composition of the moose population by sex and age caused by wolf predation and human harvest in the study area were estimated on the basis of inspection of wolf–killed prey and human harvest (Table 1). Wolf predation was disproportionately heavy on males, whereas human harvest included both sexes equally. Calves and old moose (older than 10 years) constituted 53% of the wolf kills but only 6% of the harvest by hunters (Fisher criterion F = 20.5 calculated according to Zaitsev 1984); moose in the age range of 3.5–7.5 years constituted 23 and 51% of the kills, respectively (F = 12.1). Using track size measurements (Yazan 1961), we classified the moose population in the summer of 1976 as 23% calves (<0.5 years), 11% yearlings (<1.5 years), and 66% adult (>2.5 years). In the Pripyat Reserve the age composition from 1971 to 1975 was 21.6% calves and 12.6% yearlings (Gatikh 1976). In the Berezin Reserve from 1959 to 1980, these parameters were 14.8% and 8.8%, respectively (Kozlo 1983). In June through August 1957–1977, the calf:yearling:adult ratios for moose were (%) 24:12:64 in the Leningrad region, 19:8:73 in the Novgorod region, and 28:13:59 in the Pskov region (Vereshchagin and Rusakov 1979). According to Teplov‘s data (see Yurgenson 1964) for 12 regions of Russia in 1961, the percentages in each age group ranged from 20 to 31% for calves, 6 to 16% for yearlings, and 57 to 65% for adult animals. During summer, 25% of the moose population were calves and 12% were yearlings, but in winter calves composed only 12.3% and yearlings 9.0% of the population (Vereshchagin and Rusakov 1979). Based on these findings, it appears there is a clear selection for calves in wolf predation, whereas adult moose are selectively killed by hunters. Similar results were obtained for other areas. In the Darwin Reserve wolves killed mainly young animals (61%) with no selection for sex (Kaletskaya 1973). Estimation of the proportion of kills by age on Isle Royale showed that 28% were calves, 21% animals 8–15 years of age, 38% animals 10–18 years of age, and 7% animals 20 years old (Mech 1970). According to the literature (Yazan 1961, Vereshchagin and Rusakov 1979, Filonov 1983), moose 3.5–7.5 years old have the highest reproductive activity. Thus, in the reserve, most moose preyed upon were of lower reproductive activity.

There are differences in the age and sex composition of moose killed by pairs and packs (Table 1). Males are preyed upon by pairs more frequently; no selection by sex was observed for kills by packs (the difference was not statistically significant). Kills by pairs appeared to consist of less productive moose; only 13% of all kills by

Table 1. Composition (%) by sex and age of moose killed by wolves (*n* = 79) and harvested by man (*n* = 68) in the Central Forest Reserve.

Killed	Sex		Age (years)							
by	Female	Male	<1	<2	2.5	3.5	<5.5	<7.5	<9.5	>10
Hunters	51	49	3	10	25	18	11	22	8	3
Wolves	40	60	43	4	10	3	16	4	10	10
In packs	48	52	47	6	16	5	21	5	0	0
In pairs	29	71	35	4	4	0	9	4	22	22

pairs were moose in the age range 3.5–7.5 years compared to 31% for packs, although the difference was not statistically significant. The differences in kills by pairs and packs for moose 7.5–9.5 years of age (F = 15.1) and for the animals older than 10 years (F = 15.1) are statistically significant.

Using the data on age composition of prey (Table 1), biomass values of males and females for each group (Yazan 1961), and wolf consumption level and population number, it was calculated that on average a wolf harvests 5–6 moose per year and consumes 4.75–5.75 kg of meat per day. According to observations in the study area, the consumption rate was, on average, 1 moose/7 days for a pack of 5 wolves and 1 moose/5 days for a pack of 7 wolves. Assuming that the average mass is 171 kg for a female moose and 228 kg for a male moose, one can calculate that in the first case 4.89 kg of meat were available per wolf per day, and in the second case 6.51 kg per wolf per day, the mean value being 5.7 kg/wolf/day. These approximations are very close to the consumption rates calculated above.

Thus, the moose population decline may be ascribed to both environmental and human influences, but the predominant factor was wolf predation, which exerted a pronounced effect not only on the moose population number but also on its age and sex composition.

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