HISTORY AND STATUS OF THE POPULATION DYNAMICS OF MOOSE IN THE STEPPE ZONE OF UKRAINE

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ABSTRACT: The moose (*Alces alces*) population in the steppe zone of Ukraine developed initially in 1955-1965. Early annual population growth rates were high ranging from 13-49% partly due to immigration of moose from Russia and Byelorussia. However, after fully occupying forest habitat and expanding to treeless biotopes, reproductive efficiency declined. This decline was influenced by large spatial isolation of suitable habitat; 52% of solitary males and 48% of solitary females were in isolated biotopes during breeding. Further, 8% of adult bulls were in herds without cows, and 21% of cows were in herds without bulls. Although individual productivity was good, 1.3±0.1/pregnant cow and 0.4/adult cow, isolation caused low participation in breeding (38.5% of adult cows), low number of calves (17.1% of population), and low annual population growth rate (≈ 6%/yr). The steppe moose population reached its maximum (n = 2776) in 1974 followed by steep decline; the decline was associated with harvests of 16.1% in 1973 and 12.5% in 1974, of which about 50% were adult animals. The population reached a second peak (n = 2147) in 1982 and declined gradually until 1992. A steep, annual population decline of 25.3±5.8% occurred after 1992; this decline was associated with excessive harvest beyond the annual population growth rate. Moose were extirpated from most regions of the steppe zone by the late 20th century. The current southern range of moose is limited to forest habitat, and except for a remnant population of about 80, the unique steppe population has disappeared from Ukraine.

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Moose (*Alces alces*) dispersing into southern Ukraine from adjacent forestland began to develop a marginal population in the steppe region in the mid-20th century. By 1974 this population numbered about 2,800 and primarily occupied planted forests, shelter belts, and agrocoenoses. However, most were killed by the end of the 20th century. Thus, our research was focused upon the distribution and reproductive characteristics of the remaining population to assess population dynamics under new ecological conditions.

This paper presents a summary of >25 years of data collected from 1976-2003. Because field population surveys were initiated in 1961, surveys of game-keepers and hunters were used to reconstruct earlier population estimates. Data were collected with a variety of methods including observations of moose on permanent plots, during field expeditions, and with observers in helicopter and airplane. As a result, data were collected about locations and movements at 91 points. A vast area of the steppe zone was covered where habitat use and distribution of animals (n = 639), herd composition (n = 334), and dynamics were measured. Twenty-two females were dissected to assess their reproductive state, and necropsies and field observations of mortality were conducted when possible (n = 27). We assessed spatial structure with the nearest-neighbor method (Odum 1975), and used the Ministry of Statistics of Ukraine for statistical testing and data analysis.

Dynamics of the area

Moose were widely distributed throughout Ukraine during the Paleolithic and late Stone Age. Even then moose were highly used because they were relatively easy to hunt and had high economic value. Therefore, even ancient hunters had substantial influence on moose populations. As civilization developed, hunting became the principal factor influencing the population size and distribution of moose. The First World War (1914-1917) and Socialist Revolution of 1917 changed the lives of millions of people and added to uncontrolled moose hunting. In many places moose were eliminated, and by the 1890s only about 10 remained in large forests in northern Ukraine (Migulin 1938) and a few in neighboring Byelorussia (Fedjushin 1929).

Gradual stabilization of life for the local people, renewal of work in governmental institutions, and implementation of nature conservation measures created favorable circumstances for population growth of moose in areas of the former USSR. Range expansion occurred and the southern limit extended 200-400 km in the 1940s (Geptner et al. 1961). However, this process was interrupted by World War II (1941-1945) when most moose were killed during military operations. Due to a hunting ban after the war, moose density in bordering regions of Byelorussia and Russia increased markedly and dispersal into Ukraine was common. A large inflow from the northern forests was recorded in 1947-1948 and again in 1960 (Boldenkov 1975). By 1961 moose occupied nearly the entire eastern forest-steppe zone, and some penetrated into the steppe zone and appeared in the foothills of the Carpathians Mountains (Fig. 1).

Some moose dispersed very long distances and were observed north and south of the steppe zone in the Dnieper Delta and along the coast of the Azov Sea in 1957-1962 (Filonov 1983), and even in the Danube Delta in Romania in 1964 (Almeshan 1966). By 1962 their range boundary shifted to the south along the Dnieper floodplain for 350-500 km, and along the Seversky Donets floodplain for 200-250 km (Galaka 1964). Unfortunately, initial migrants were often tolerant of people and the majority often succumbed to poaching. Dispersal slowed afterward and reduced numbers were found in the large river valleys where floodplains were considerably transformed in the steppe zone. Dispersal was also slowed by the small area of forest habitat intermingled with vast areas of non-habitat (i.e., arable land;Table 1).

By 1966 the southern range limit moved to the forest-steppe zone in western Ukraine, however many animals were previously south of this limit (Fig. 1). In the eastern steppe zone moose completely occupied forests in the Seversky Donets River Basin and along the Dnieper tributaries. Later in 1967-1980, moose occupied shelter belts, planted forests, and fields in areas adjacent to the Sea of Azov and the Black Sea; some even penetrated to the Crimean Peninsula in 1971 and 1976 (Dulitsky 2001). By 1980 the southern range boundary had reached its contemporary limit in Ukraine. Forest habitats were already occupied by moose, and further expansion to the south was not recorded, although occasional observations were noted in the late 20th century.

During development of the steppe population, the distance between core areas quickly contracted and reached a minimum by

Table 1. Characteristics of land occupied by moose in the steppe zone of Ukraine (1000s ha).

Administrative region	Total area	Arable land	(%)	Forest	(%)
Lugansk	2670.0	1458.0	(54.6)	155.8	(5.8)
Dniepropetrovsk	3190.0	2155.0	(67.6)	78.9	(3.7)
Donetsk	2650.0	1686.0	(63.6)	94.2	(3.6)
Odessa	3330.0	2081.0	(62.5)	72.6	(2.2)
Kherson	2856.0	1712.2	(60.0)	45.0	(1.6)
Zaporozhye	2730.0	1944.0	(71.2)	42.8	(1.6)
Nikolayev	2450.0	1716.0	(70.1)	23.0	(0.9)
Total:	19876.0	12752.2	(64.2)	512.3	(2.6)

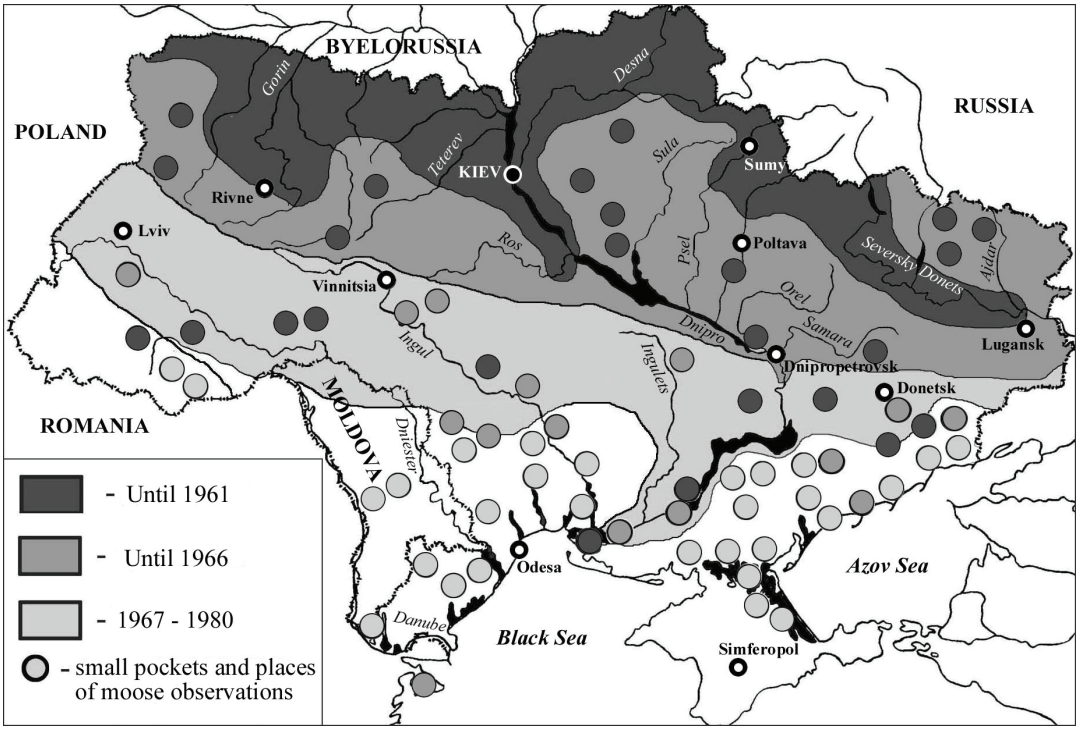


Fig. 1. The chronology and location of the southerly dispersal and expansion of the moose population in Ukraine during the 20th century.

the1980-90s. The extreme limit was defined by the distance between forest biotopes, and by territorial and trophic competition. In some areas of the steppe zone moose inhabited agrocoenoses or forest belts 3-5 km apart. By the end of the 20th century, moose were exterminated everywhere due to excessive hunting and poaching, and their southern range retracted northward to the forest-steppe and steppe zones. During that process the distance between separate micro-populations and single moose increased greatly to 100s of km (Table 2).

In summary, the following dynamics of moose range were observed in Ukraine during the 20th century:

1) reduction due to poaching and habitat loss occurred from periphery to refuge areas; restoration occurred vice versa,
2) all new pockets of moose developed only in forestland,
3) some initial dispersers were atypically tolerant of people and suffered high mortality,
4) dispersal occurred along a broad front, but major routes were along river valleys and forestland, and
5) expansion of moose range occurred when the population density was both high and low.

Table 2. Spatial structure of the steppe moose population during 3 phases of population dynamics in southern Ukraine. Data are distances (km) between pocket areas or areas of prolonged occupation.

Phase	Years	n	Mean ± SE	Range
Occupation	1955-1971	47	107.6 ± 9.1	13.1 – 300.2
Peak population	1980-1990	30	24.4 ± 5.7	3.1 – 135.0
Depressed population	1993-2003	14	125.7 ± 7.0	90.1 – 183.2

Reproduction

Moose reproduction was maximal in the steppe zone of Ukraine during the period of its highest population (1981-1990, Table 3); however, during expansion and dispersion the population essentially declined. Possibly, this was related to the dominance of young females in the population that are less fertile than animals of middle age (Filonov 1983). The mean calving rate was 1.3 ± 0.10/pregnant or 0.4/adult female (Volokh 2002). On average there were 78% singletons, 25% twins, and 3% triplets; however, the adult reproductive rate was only 39%. In comparison, this rate was 46% north of and 69% south of the forest zone in Russia, with 1.2-1.4 embryos/pregnant female and 0.6-1.1 embryos/adult female (Filonov 1983). An analysis of 27,300 licenses from harvested females indicated embryo/adult female ratios of 1.2-1.4 in European Russia and 1.3 in the forest-steppe and steppe zones. In the latter case, the proportion of pregnant females to adults was 0.3-0.8 (Rozhkov et al. 2001), which was similar to the fertility rate of moose at their southern range in the steppe region of Ukraine. It is interesting that reproductive rates were 80-100% along the northern border of moose range in Finland (Rajakoski and Koivisto 1970), and fertility fluctuated from 0.3 for young animals to 1.1 for animals of middle age (Nygren et al. 1999).

The majority (69%) of the marginal population in southern Ukraine was adult animals in very small groups (herd) (Table 4); in comparison, 74% were adults in northwest Russia (Vereschagin and Rusakov 1979) and 76% in Byelorussia (Kozlo 1983). Few were aged 2 years (9.7%) which presumably was a result of high mortality of young animals and low productivity.

Table 3. Reproductive indices of the steppe moose population in southern Ukraine.

Year	Number of adult females		Number of calves/ pregnant female	
	total	with calf (%)	Mean ± SE	Range
1971-1980	76	28 (37)	1.25 ± 0.08	1 – 2
1981-1990	83	37 (45)	1.40 ± 0.10	1 – 3
1991-2002	75	25 (33)	1.28 ± 0.11	1 – 2
Total:	234	90 (39)	1.33 ± 0.10	1 – 3

Maximum birth rate (25-26%) is achieved at an adult sex ratio of 1 ♂:0.9-1.1 ♀ (Filonov 1983). The birth rate was 24.2% in a population with sex ratio of 1:1 in the forest-steppe zone of Russia (Pobedynskij 1990), 18.0% in a population with a sex ratio of 1:1.4 in the forest zone (Filonov 1983), and 14.8% in a population with sex ratio of 1:0.9 in Byelorussia (Kozlo 1983). There was considerable dominance of females (1 ♂:1.4 ♀) in the northern steppe zone of Ukraine with small isolated forests. The proportion of calves was 21.8%, similar to the rate reported in Canada (21%; Peterson 1955). In southern Ukraine the sex ratio was nearly optimal (1 ♂:1.2 ♀) only in forest biotopes, whereas in open landscapes males were dominant (1.6 ♂:1 ♀). Further, many solitary adult moose were observed (n = 205; Table 5); because many (107 males and 98 females) were in isolated biotopes considerable distances apart, reproduction was affected negatively. There were 22 adult males (8.4%) in biotopes without adult females, and 53 females (20.6%) were likewise isolated. This isolation contributed to both low annual population growth (about 6%) and calf production (17.1%).

Low reproductive rates were caused by isolation of forest habitats preventing animal exchange, as well as different reproductive strategies of males and females. At the southern border of their range, adult females are usually long-term occupants of isolated forest habitats, island-like among agrocoenoses, and move little during the breeding season. Conversely, males often disperse widely searching for females and forest habitats, sometimes reaching the seashore; many perish, mostly from poaching. We identified traits of gunshot wounds in 47% of mortalities (n = 62). Unfortunately, this information was not considered when harvest regulations were developed for exploiting the

Table 4. Age structure and group (herd) size of the steppe population of moose at the southern range limit in Ukraine.

Age and sex	Total		Herd Characteristics		
	#	%	#	moose/herd ± SE	Range
Adult males	208	32.6	190	1.09 ± 0.03	1-5
Adult females	234	36.7	197	1.19 ± 0.05	1-4
Yearlings	62	9.7	54	1.15 ± 0.09	1-3
Juveniles	134	21.0	90	1.49 ± 0.14	1-6
Total:	638		334		

southern moose population, and contributed to its extirpation (Volokh 2002).

Population dynamics

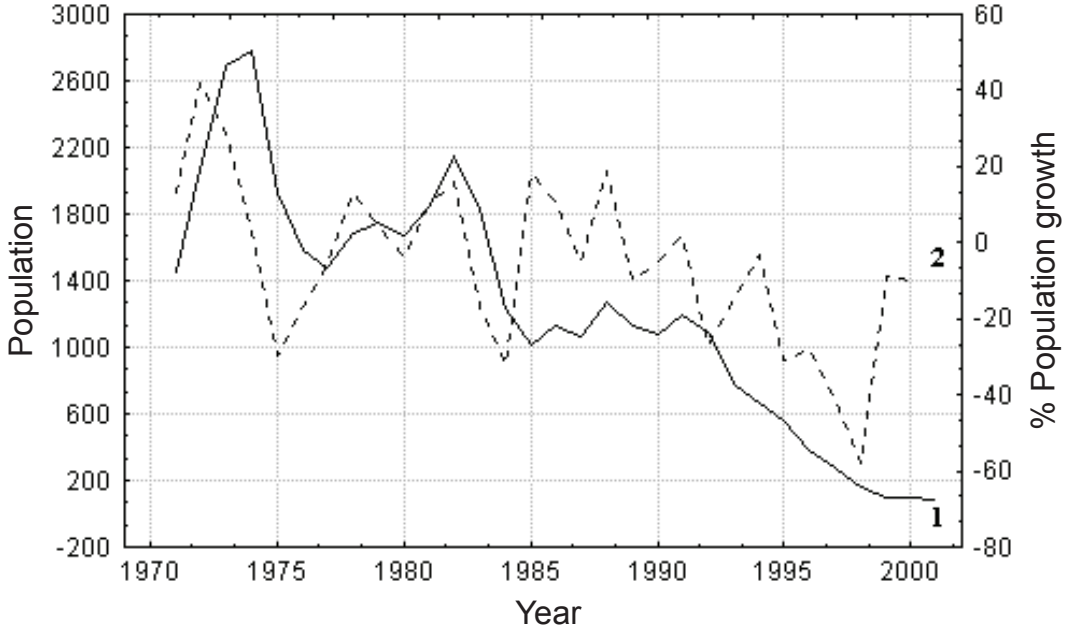
Humans invariably have strong influence on population size of hoofed animals, including moose. The developing moose population in the steppe zone of Ukraine was related to an initial increase of resources in neighboring Byelorussia (Kozlo 1983) and Russia (Filonov 1983), and later in the forest zone of Ukraine. Moose hunting began in 1946 in the European part of Russia, and the population and harvest increased concurrently; in 1960 there were 9,200 moose harvested, and by 1962 the harvest was 21,300 (Filonov 1983). Moose were first hunted in Byelorussia in 1965, and about 30,000 were shot in 30 years (Kozlo 1983). The associated reduction in moose density caused less emigration into the forest zone of Ukraine where an initial harvest of 60 moose occurred in 1965. Population growth rate was high along the southern range border reaching 28% (13-49%), similar to that in the forest zone (Fig.2), as well as throughout Ukraine in the 1960s (25-26%; Boldenkov 1975). This high growth rate resulted from high reproduction of local animals and immigration.

It should be noted that the dynamics of the moose population throughout Ukraine was notable for its synchronism (Fig. 3). The time period between the initial hunt (1965) and when the maximum population was reached in each area of the steppe zone was nearly identical, 15.3±0.6 years. This was irrespective of area or location, relative isolation, and relative distance to refuges occupied with moose. It was evidence of the strong influence of the

Table 5. Distribution and herd composition of the moose population in biotopes at the southern range of moose in Ukraine.

Biotope	Single adult moose			Herd composition		
	Total	% Male (n=107)	% Female (n=98)	Adult:total	% Male only (n = 13)	% Female only (n = 18)
Deciduous wood	74	36.5	63.5	51:89	5.9	13.7
Coniferous wood	26	53.9	46.1	18:37	27.8	11.1
Forest belt	29	72.4	27.6	19:36	5.3	10.5
Plavni	22	63.6	36.4	20:31	10.0	15.0
Field	21	71.4	28.6	14:34	7.1	7.1
Garden	12	41.7	58.3	6:15	16.7	16.7
Gully	11	45.5	54.5	3:6	-	33.3
Steppe	6	83.3	16.7	2:3	-	-
Reed beds	4	25.0	75.0	3:5	-	33.3
Total or average:	205	52.2	47.8	136:256	8.4	20.6

Fig. 2. The estimated size (1) and % growth (2) of the moose population in the steppe zone of Ukraine, 1970-2000.



migration rate and effective reproduction in an anthropogenic landscape.

The moose population reached maximum (n = 2776) in the steppe zone of Ukraine in 1974 (Fig. 3). Most (>57%) occupied the Lugansk region, almost 23.5% the Donetsk region, >9.4 % in Dniepropetrovsk, and the remaining few were in other regions (Table

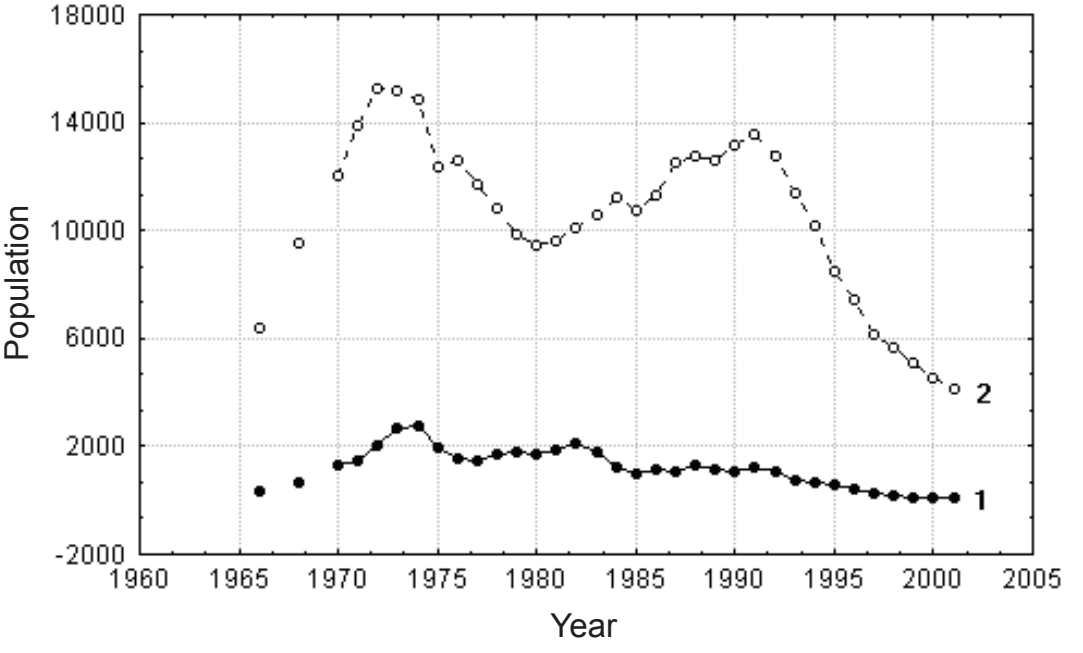


Fig. 3. Comparison of the moose population in the steppe zone (1) with other areas of Ukraine (2), 1965-2002.

Table 6. Chronology of the population estimates of moose in 7 regions of the steppe zone of Ukraine. The initial population estimate in each region occurred in the time period 1955-1965.

Location	Maximum population (year)	Population - Jan. 2003 (% decline)
Odessa	65 (1979)	0 (100)
Nikolaev	26 (1974)	0 (100)
Kherson	64 (1976)	0 (100)
Zaporozhye	120 (1974)	0 (100)
Dniepropetrovsk	260 (1973)	5 (98)
Donetsk	670 (1973)	31 (95)
Lugansk	1595 (1973)	46 (97)

6). In that period the population density was so high in most forestland of the steppe zone that individual home ranges often overlapped, and damage was high on forest plants difficult and expensive to grow in dry southern regions. Consequently, moose were hunted even in areas with low population density. However, instead of reasonable management of this valuable resource, hunting was based on maximum harvest for monetary profit from domestic and export meat markets.

With harvest rates equal to 4.3-8.1% of the annual population, hunting had minimal influence on population density. However, a measurable population decline occurred after harvest rate increased to 16% in 1973 and 12.5% in 1974. This negative situation was apparently managed for and in 1982 the steppe population reached its second peak (2,147); however, in 1981-1984 the population fell >50%. In 1985-1991 the population stabilized at 1,000-1,200, with small increases observed in 1986, 1988, and 1991. Since 1992 a steady and rather quick population decline (25.3$\pm$5.80% annually) occurred throughout the steppe zone (Fig. 2).

By the end of the 20th century moose had disappeared in the Zaporozhye, Odessa, Nikolayev, and Kherson regions, and only about 80 animals remained in the Dniepropetrovsk, Donetsk and Lugansk regions (Table 6). Presently, primary moose habitat is floodplain forests of the Samara and the Seversky Donetsk Rivers in the steppe zone of Ukraine. Excessive hunting also caused considerable reduction (69-98%) of the population in the forest-steppe zone. Further, many local populations were lost in areas (mostly forest habitats) with the highest numbers and density. Although moose hunting is prohibited except for a few selected individuals (3 in 2001 and 8 in 2003), population growth has not been realized; the estimated population was 4950 in 2000 and 4490 in 2003.

The primary reason for the moose population decline in the steppe zone was that the exploitation rate greatly exceeded the average annual growth rate. Although only about 8% of the population was harvested annually in Ukraine, more than half the harvest was adult animals (Krizhanovskij et al. 1988) that ultimately caused lower productivity. Importantly, this harvest estimate does not account for wounding and poaching mortality. In total, human-associated mortality was undeniably the most important factor influencing the population dynamics of moose and all hoofed animals in Ukraine in the late 20th century.

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