FRAGMENTATION OF EURASIAN MOOSE POPULATIONS DURING PERIODS OF POPULATION DEPRESSION

Taras P. Sipko and Marina V. Kholodova

Institute of Ecology and Evolution, Russian Academy of Sciences, 33 Leninsky Prospect, Moscow 119071, Russia

ABSTRACT: Changes in the distribution of Eurasian moose (*Alces alces*) populations during the Pleistocene and Holocene eras were analyzed from historical and contemporary literature. We focused on how range boundaries varied, suitable habitat was fragmented, and how local and regional populations were isolated, especially during periods of population depression. We discuss how the occurrence and duration of isolation of local populations likely influenced the genetic structure of Eurasian moose. We question the geographic division of certain subspecies, and suggest that our analysis be used to reinterpret and revise genetic structure of Eurasian moose populations.

ALCES VOL. 45: 25-34 (2009)

Key words: *Alces alces*, Eurasia, fragmentation, genetic structure, history, isolation, moose, population depression, range, subspecies.

The Eurasian moose (*Alces alces*) population returned to most of its original range during the 20th century. Historically it experienced numerous range reductions and fragmentations that were followed by restoration and dispersal into new areas. Recent research (Danilkin 1999) suggests that species differentiation in moose could be greater than believed previously. In order to best understand and interpret the genetic structure of Eurasian moose (i.e., its phylogeography and polymorphism), it is necessary to identify dispersal centres where genetic diversity was presumably highest. Assuming that mitochondria are inherited maternally and females disperse shorter distance than males, we expect that the geographic distribution of mitochondrial DNA haplotypes was fairly stable and should reflect past migration routes of moose. We collected and analyzed extensive archaeological and paleontological data to trace moose range during periods of substantial population depression. We regard our results as preliminary because these data are incomplete, and distribution of moose populations varied in space and time and was not always documented accurately.

DISTRIBUTION AND TAXONOMOY

Subspecies of moose in Eurasia are considered to have no distinct differences; variable morphological characteristics relative to geographic location represent a cline (Markov and Danilkin 1996, Danilkin 1999). Moose constitute one macropopulation in Europe (Rozhkov et al. 2002, Davydov et al. 2004) with European moose (*Alces alces alces*) inhabiting Europe, Altai, and western Siberia up to the Yenisei River (Danilkin 1999). In summer and winter the Yenisei River is a stem of a large river system rich in valleys that are preferred moose habitat with no hindrance to moose migration. We suspect that the subspecies boundary lies either westward along the Ob and Yenisei Rivers divide, or eastward along the divide of the Yenisei and Lena River basins; further research is required to better delineate this boundary.

Caucasian moose (*A. a. caucasicus*) in the Caucasus area were eliminated by the beginning of the 20th century. Repopulation of the north Caucasus region by this subspecies in the 20th century indicates that Caucasian and European moose habitats were probably well

connected in the past, and calls into question whether to identify Caucasian moose as a separate subspecies (Danilkin 1999). The subspecies status seems more appropriate for the moose population in the westernmost part of Europe.

Yakut moose (*A. a. pfizenmayeri*) inhabit the area to the east of the Yenisei River up to the Stanovoi Ridge, Khakassia (Tikhonov 1990), northern Mongolia to the south, and the Tchersky or Verkhoyansky Ridges to the northeast. Kolyma moose (*A. a. buturlini*) are distributed in northeast Siberia to the east of the Tchersky Ridge (Zheleznov 1990). We think that the boundary of this subspecies runs along an arc formed by the Verkhoyansky Ridge and Subtar-Khayata Ridge; further genetic research is needed to delineate this boundary.

Ussuri moose (*A. a. cameloides*) are restricted to the southwestern part of Siberia and the Amur basin; the distribution of this subspecies requires further study. It's highly possible that moose populations inhabiting the area east of Baikal Lake (Ditsevich 1990) and further east in steppe valleys of the Selenga and Orkhon basins, and in northeast China also belong to this subspecies. The northern boundary runs along the Stanovoy Ridge (Kutcherenko 1975) and the Lena River divide (Danilkin 1999).

BIOLOGICAL PARAMETERS

In Russia moose live mainly in forest habitats but also occupy the forest steppe and forest tundra. Moose were documented in tundra on the Lena River estuary along the coastline of the Arctic Sea (Nasimovich 1955), and moose remnants were found on New Siberian Islands in the Arctic Sea (Vereshchagin 1967). They were also documented in the desert near Aral Lake, >500 km from their original ecotopes (Heptner and Nasimowitsch 1974). Moose have also been documented in the alpine zone to 2500 m elevation (Semenov-Tjan-Shansky 1948, Heptner et al. 1961). Although typically sedentary, certain populations migrate and individuals may disperse long distances. It took them several decades to disperse >1500 km to reach the Caucasus foothills (Yasan 1966), but they easily cross waterways 10-15 km wide (Timofeeva 1974). Their size, mobility, and relatively high reproductive rate aid them in repopulating vacated areas.

MOOSE IN THE PLEISTOCENE ERA

The earliest evidence of moose remains dates back to the mid-Pleistocene era (Vereshchagin 1967) that had no less than 3 periods of glaciation (Gerasimov and Markov 1939) that dramatically altered landscapes and moose range (Fig. 1). According to Vereshchagin (1967), there is scarce evidence of moose in the Ice Age, whereas moose remains are considerable in the Holocene era. Active morphogenetic processes apparently occurred in the late Pleistocene era (Boeskorov 2001).

Moose distribution during the Ice Age can be described only in general terms. Because the greatest part of Europe was covered by glacial sheets and lakes, moose probably inhabited a rather narrow territory between the ocean and glacial lakes adjoining the Alpine and Nordic ice sheets. This was possibly a connecting link between the moose population in southwest Europe overgrown with forests very much like those of modern Scandinavia (Woillard 1979), and that inhabiting vast areas of the South Ural Mountains where forest refugia existed (Panov 1999). The European moose population in this area seems to be the most abundant and genetically diverse, and as the glacial sheet retreated northward it covered Eastern Europe.

Much later, about 10,000 years ago when the southern part of Scandinavia was free of ice, European moose with red deer (*Cervus elaphus*) and wisent (*Bison bonasus*) found their way from West Europe to Fennoscandia using Denmark as a land bridge (Filonov 1983), and later dispersed from the east through the Karelian Isthmus. In West Siberia when

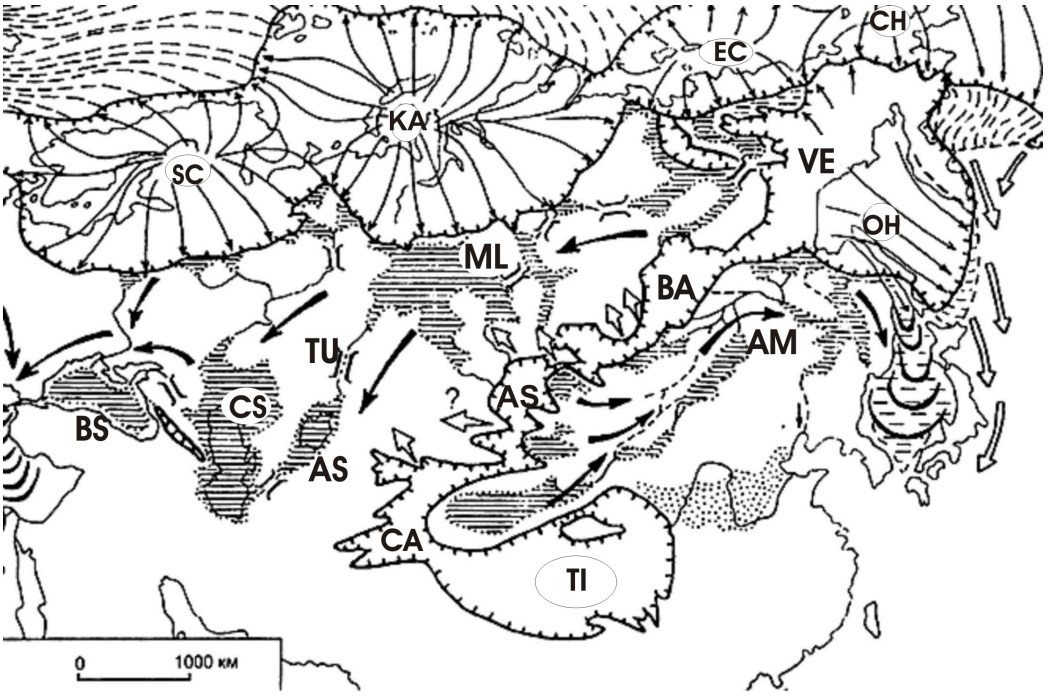

Fig. 1. Distribution of ice sheets, mountain glaciers, and ice-dammed lakes in Eurasia during the mid-Pleistocene era (according to Groswald 1984) that influenced the distribution and range of moose. Major seas include the Aral (**AS**), Black (**BS**), and Caspian (CS). Glacial sheets include the Chukchi (CH), East Siberian (ES), Karskii (KA), Ohotskii (OH), and Scandinavian (SC). Mountain glaciers include the Altai (AS), Baikal (**BA**), Central Asian (CA), Tibetan (TI), and Verkhoyansk (**VE**). Other features include Lake Mansijskoe (**ML**), Amur River (**AM**), and the Turgaiskii trench (**TU**).

the last glacial period was at its utmost, the glacier blocked the Yenisei and Ob Rivers forming Mansi Lake, a large reservoir twice as large as the Black Sea; surplus water ran via the Turgai Channel to the Caspian Sea (Groswald 1983). During this period western and eastern Siberian moose appeared to be totally isolated, which explains the chromosomal differences between the eastern and western populations. The Altai-Sayan mountain region had no solid glacial sheet during the Ice Age (Gerasimov and Markov 1939), although a chain of mountain glaciers factored into the isolation of northern and southern moose populations in this area. There was no solid glacial sheet in East Siberia during the Pleistocene (Groswald 1998, 1999) and moose occupied all suitable areas.

Southeast Siberia is limited by Lake Baikal in the west and by the Stanovoi Highlands, then the Stanovoi Range, and part of the Dzhugdzhur Range in the east. Although moose currently cross these mountain systems, these mountains were covered with vast glaciers in the Pleistocene era (Preobrazhenskiy 1960, Groswald 1984) and were impassable for some period isolating the so-called Ussuri moose from the rest of the population.

Northeastern Asia is a huge amphitheatre sloping towards the Arctic Ocean that is characterized by strong orographic contrasts; though subdued mountains prevail, they are joined with highlands and plains. The Verkhoyansk Mountains present an orographic barrier of the area in the west. To the south of the Verkhoyansk Range, the Sette-Daban and the Yudom Range stretch divided by the Yudom-Mai Highlands, and further along the Okhotsk Sea coastline lies the Dzhugdzhur Range. The Tchersky Range stretches 1800

km northwest to the east of the Verkhoyansk Mountains. Glaciers developed in the mountains to various extant and during glacial maximums reached highland valleys which had several glacial and interglacial periods (Groswald and Kotljakov 1989). Highlands occupy the inner part of the area, and lowlands lie along the coast and narrow stretches penetrate between the mountains to the south. These valleys formed refugia where isolated moose populations survived. Four moose populations that formed during the Ice Age are documented in the area (Safronov 2008). Further, during the Sartan Ice Age there was a forest refugium in the middle reach of the Anadyr (Kozhevnikov and Zheleznov-Chokotskij 1995) where a moose population most closely related to Alaskan moose might have existed.

RANGE RECESSION IN EURASIA

Moose were distributed across most of Europe during the early Holocene era (Heptner et al. 1961, Vereshchagin 1967). Later the range retreated eastward; the last moose was killed in Saxony in 1777 and in Galicia in West Ukraine in 1769 (Gebel 1879). By the end of the 18th century moose were eliminated in Belovezhskaya Pusha (Sablina 1955). In the beginning of the 20th century moose were still in East Prussia (now Kaliningrad region, Russia; Obermeier 1913) but were never encountered after World War I. Thus, the European moose was preserved only in Russia and the Nordic countries by the mid-20th century.

European part of Russia

During the period of utmost population depression, the southern boundary of moose range retreated 450-1000 km northward, the northern boundary 500-600 km southward (Danilkin 1999), and the range was fragmented (Fig. 2). The northern boundary corresponded to the northern extent of the forest zone and reached 65° N in the Ural Mountains (Sokolov 1959). The southern boundary coincided with the latitudinal flow of major rivers such as the Volga, Kama, and Belaya Rivers (Filonov 1983). Figure 2 depicts the location of 20 isolated moose populations; in the following text each population is described both temporally and geographically with an accompanying number [#] identified on Figure 2.

The main area was divided roughly into western [1] and eastern parts [2] along the Vologda-Arkhangelsk railroad and the White Sea-Baltic Canal; there is no information regarding the duration of this fragmentation. The western part was characterized by irregular moose distribution of variable configuration and included the Leningrad, Pskov, Novgorod, and Tver regions, the western part of the Vologda region, the northern part of the Smolensk region, and north of Byelorussia (Serzhanin 1961).

There is good reason to believe that a small breeding population survived in the area of the Pripyat and Pinsk [3] marshes (Serzhanin 1961, Galaka 1964). A small population of moose also survived in the Bryansk forests [4] along the left bank area of the Desna River (Fedosov and Nikitin 1951) and moose were also documented in the Sumy region (Galaka 1964). Moose also survived extirpation in the Meshcherskaya Lowland [5], the boggy interfluve of the Volga and Oka Rivers (Severtsev 1854, Kulagin 1932). One other isolated population existed in the area between the Tsna and Sura Rivers [6] in the Mordovia, Penza, and Tambov regions (Filonov 1983).

Scandinavian Peninsula

Current Norwegian and Swedish moose populations are abundant, yet in the beginning of the 19th century only small, isolated groups survived in the southwest of the Scandinavian peninsula [7] (Markgren1974, Danell and Bergström 2008). The same situation occurred in Finland where moose disappeared by the mid-19th century (Markgren1974, Nygrén et al. 2008). Single animals migrated gradually

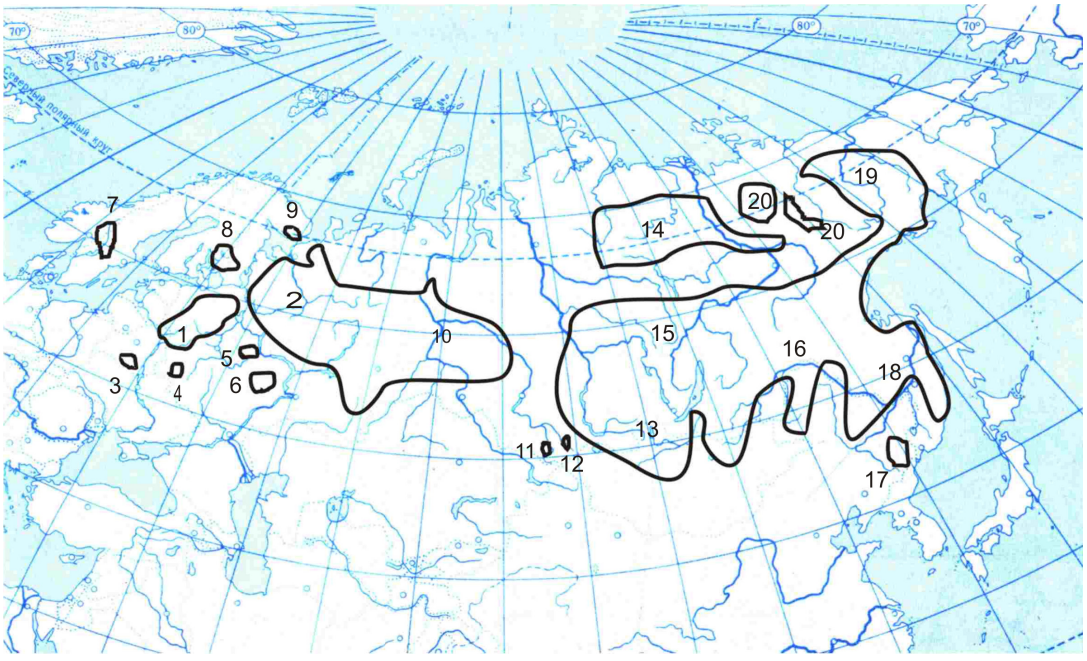

Fig. 2. The southern boundary of moose range retreated 450-1000 km northward and the northern boundary 500-600 km southward during the period of severest population depression, This figure identifies the location of 20 isolated moose populations during this period; each population is described both temporally and geographically in the text.

from adjoining regions of South Karelia [8] where the moose population was not abundant (Vereshchagin and Rusakov 1979). Data on the Kola Peninsula [9] is rather contradictory. Some authors (Semenov-Tjan-Shanskij 1948, Kirikov 1966) state that the species disappeared from the area and later repopulated it from adjoining territories. Others (Vereshchagin and Rusakov 1979) quote data supporting that a moose population survived on the peninsula.

West Siberia

The moose population between the Ural Mountains and the Yenisei River in West Siberia [10] was at its minimum by the beginning of the 1920s. The northern boundary arched southward reaching 63° N, and the range was a strip of land about 450 km wide (Laptev 1958), with a 250-500 km wide gap in the region of the Ob River dividing the area into eastern and western parts (Laptev 1958, Yurlov 1965). It is suggested that migration could occur between these areas, but insufficient evidence exists to support or refute this idea. This gap existed for an unknown period, but we believe it lasted no less than 100 years.

South Siberia

The moose population of the Altai-Sayan Mountains was at its minimum at the end of the 19th century (Sobansky 1975). Moose were also eliminated in the adjoining regions lying to the north and northwest in the Kemerovo region in Kuznetsk Alatau (Sobansky 1992), in the South Altai, and the adjoining Kazakhstan regions (Sludsky 1953). Moose were considered fully extirpated in Altai (Filonov 1983), nevertheless, a small population may have possibly survived in the upper reaches of the Abakan, Biya [12] (Dmitriev 1938), Katun, and Tchuya Rivers [11] (Sobansky 1975). Repopulation of the Altai region resulted from migration from both the east and west (Filonov 1983).

Moose was never abundant in the Sayan

region. In the beginning of the 20th century they disappeared from the Khakas-Minusinsk basin (Skalon et al. 1941), as well as from the West Sayan where only single animals were encountered migrating from the west. Moose survived only in the East Sayan, east of Tuva, and in the eastern part of the Tannu-Olu Range [13]; the latter were connected with a Mongolian population (Yanushevich 1952).

The Mongolian population occupied the area south of the Altai-Sayan region and was limited to mountainous taiga regions. Moving west to east, moose left in the Mongolian Altai were encountered only at the beginning of the eastern part of the Tanu-Ola Mountains. Further east moose occupied an area around Habsugul Lake, the Khangai Mountains up to the Khabgai-Nuru Range in the south, and the upper reaches of the Onon, Kerulen, and Tola Rivers and other rivers in the Khantae Uplands (Bannikov 1954).

East Siberia

This region was a northern Siberian upland between the Yenisei and Lena Rivers where the distribution of moose has changed considerably (Michurin and Mironenko 1967). During the period of lowest population at the end of the 19th-early 20th centuries, the range boundary crossed the Yenisei River at 59^0 30' N and went northeast crossing the Podkamennaya Tunguska River. It followed the Verkhnyaya Tunguska and Podkamennaya Tunguska divide to 100^0 E, where it turned north to the upper reach of the Kotui River basin, went along the Kotui to 70^0 N, and then east to the mid-reach of the Anabar River [14] (Naumov 1934, Heptner et al. 1961).

According to Middendorf (1869), in the mid-19th century moose were occasionally documented along the banks of the Nizhnyaya Tunguska River. However, Maak (1887), whose expedition in 1854–55 visited the Vilyuy River starting not far from the Nizhnyaya Tunguska River that flows east to the Lena River, reported that moose were absent in the area and local people had no knowledge of them. Moose were also absent in central Yakutia (Tavrovsky et al. 1971). We suggest that northern [14] and southern [15] populations in this region were isolated for an extended period.

Southeast Siberia

Moose range has changed little in the region of the Trans-Baikal and Amur Basin [16]. The southern boundary along the Sea of Japan retreated northward to 44^0 45' N (Kaplanov 1948), and moose abandoned the Ussuri and part of the Amur bottomlands [18] (Zhitkov 1914, Rakov 1965). More apparent changes occurred in southwestern China where at the beginning of the 20th century moose were distributed to the north of the Chita-Kharbin-Vladivostock railroad (Oshanin 1934, Zhen Zuoxin 1956). They inhabited the Great and Little Khingan Mountains and were in direct contact with moose on the opposite bank, often crossing the Amur River (Rakov 1964). Thus, this Chinese population and the adjacent Russian population should be considered the same.

One other population survived in East Manchuria at the interfluve of the Ussuri and Sungari Rivers [17] (Abramov 1949); it was isolated long enough to develop different antler morphology than moose in the Sikhote Alin (Rakov 1965). Further, in an east [18]-west [16] direction along the Chita–Khabarovsk transect, average body weight increases stepwise to the west boundary of the Khabarovsk Territory (Rozhkov et al. 2001) where the Little Khingan meets the Bureinsky Range. It is possible that these mountain ranges divide genetically and taxonomically different moose populations.

Northeast Siberia

Moose disappeared before the beginning of the 18th century in the Kamchatka Peninsula (Vereshchagin and Nikolaev 1979) and Sakhalin Island (Kozyrev 1960, Alekseev 1974)

where none were documented by the first Russian explorers. In the 1820s moose were rare in the whole region (Mensbir 1878) and were not documented in the Koryak District (Fil and Demyanyuk 1972). The range boundary along the Pacific coast retreated westward to the Kolyma tributary of the Omolon River [19] (Zheleznov 1990, Sipko et al. 2004). Moose did not inhabit the central axial zone of the mountain ranges of the Verkhoyansk Uplands (Tavrovsky et al. 1971), though some survived in mountain valleys [20] forming 4 isolated populations (Safronov 2009). Repopulation of the Kamchatka Peninsula occurred from recent transplants (Sipko et al. 2004, 2008).

CONCLUSION

Moose range in Russia underwent repeated changes during the Pleistocene and Holocene eras in response to climatic and landscape changes. This complicated geographic history caused periods of isolation for particular local moose populations. Some isolated populations were depressed severely and probably passed through a genetic bottleneck that influenced their local genetic structure. Because certain populations demonstrate distinct morphological and physical differences, we suggest that the taxonomic and phylogenetic structure of moose range in Eurasia is more complex than considered previously. Further genetic studies of distinct populations would help elucidate such genetic relationships and differences.

REFERENCES

Abramov, K. G. 1949. The distribution, ecology, and economy of moose in Priamurie. The Nature Branch of Biology 54 (1): 17-28. Moscow, Russia. (In Russian).

Alekseev, A. I. 1974. The Amur Expedition, 1849-1855. Publishing House of Nauk Academy, Leningrad, Russia. (In Russian).

Bannikov, A. G. 1954. The Mammals of the Mongolian People's Republic. Publishing House of the Academy of Sciences of USSR, Moscow, Russia. (In Russian).

Boeskorov, G. G. 2001. Systematization and Origin of Modern Moose. Siberian Branch of the Russian Academy of Science, Novosibirsk, Russia. (In Russian).

Danell, K., and R. Bergström. 2008. The history of moose management in Sweden - an 800 year perspective. 6th International Moose Symposium, Yakutsk, Russia, 14-20 August, 2008. Abstract only.

Danilkin, A. A. 1999. The Deer (*Cervidae*), Mammals of Russia and Adjacent Regions. Moscow, Russia. (In Russian).

Davydov, A. V., O. P. Piskunov, A. V. Pronjaev, and J. I. Rozhkov. 2004. Spatial differentiation moose of Eurasian moose by results of an estimation of the hunting trophies. Bulletin of Game Biologists 1: 36-41. Moscow, Russia. (In Russian).

Ditsevich, V. N. 1990. Systematization and morphology of East Siberian moose. 3rd International Moose Symposium. Syktyvkar, Russia, 27 August-5 September. Abstract only.

Dmitriev, V. V. 1938. Ungulates of the Altaisky Nature Reserve and surroundings (east Altai and west Sayan). The Altay Reserve 1: 171-262. (In Russian).

Fedosov, L. V., and K. N. Nikitin. 1951. Pages 6-8 *in* Fauna of the Bryansk Area. Bryansk Publishing House, Bryansk, Russia. (In Russian).

Fil, V. I., and V. P. Demjanjuk. 1972. Distribution and number of moose in the Kamchatka area. Russian Scientific Research Institute of Hunting and Fur Farming 34: 32-36. Kirov, Russia. (In Russian).

Filonov, K. P. 1983. Moose. Lesnaya Promyshlennost, Moscow, Russia. (In Russian).

Galaka, B. A. 1964. Expansion of moose range in Ukraine. Pages 35-43 *in* Biology and Economy of the Moose. Rosselhozizdat, Moscow, Russia. (In Russian).

Gebel, G. 1879. Influence of the person and its culture on an empire of animals. Nature

and Hunting 1: 95-117. Moscow, Russia. (In Russian).

Gerasimov, I. P., and K. K. Markov. 1939. The Glacial Age in Territory of the USSR. Works of Institute of Geography, Vol. 33, Academy of Sciences, Moscow–Leningrad, Russia. (In Russian).

Groswald, M. G. 1983. Integumentary glaciers of continental shelves. Science, Moscow, Russia. (In Russian).

_____. 1984. The Euro-Asian glacial cover. Pages 130-131 *in* Glaciology - the Dictionary Gidrometeoizdat. Leningrad, Russia. (In Russian).

_____. 1998. Materials Glaciology. 84: 121-129. Moscow, Russia. (In Russian).

_____. 1999. Euro-Asian Hydrosphere Accidents and a Congelation of Arctic Regions. Moscow, Russia. (In Russian).

_____, and V. M. Kotljakov. 1989. Great glacial systems and drain of Northern Eurasia and its significance for inter-regional correlations (Quaternary Period). Paleogeography and Litologia 5-13. Kishinev, Shtiincza, USSR. (In Russian).

Heptner, W. G., and A. A. Nasimowitsch. 1974. Der Elch (The Moose). Ziesmanverlag, Wittenburg Lutherstadt, Germany. (In German).

_____, A. A. Nasimovich, and A. G. Bannikov. 1961. Mammals of the Soviet Union. Artiodactyls and non-Artiodactyls. Moscow, Russia. (In Russian).

Kaplanov, L. G. 1948. Tiger, red deer, and moose. Otdelenia Zoologia No. 14 (29). Moscow, Russia. (In Russian).

Kirikov, S. V. 1966. Hunting Animals, Natural Environment, and Man. Nauka, Moscow, Russia. (In Russian).

Kozhevnikov, J. P., and N. K. Zheleznov-Chukotskij. 1995. Beringia: History and Evolution. Moscow, Russia. (In Russian).

Kozyrev, R. V. 1960. The Ancient Past of Sakhalin. Yuzhno-Sakhalinsk, Russia. (In Russian).

Kulagin, N. M. 1932. Moose of the USSR. Publishing House of Nauk Academy, Leningrad, Russia. (In Russian).

Kutcherenko, S. P. 1975. The distribution, number, and use of Ussurijskogo moose. Pages 108-109 *in* Ungulate Fauna of the USSR. Moscow, Russia. (In Russian).

Laptev, I. P. 1958. Mammals of a Taiga Zone of Western Siberia. Tomsk University Publishing House, Tomsk, Russia. (In Russian).

Maak, R. K. 1887. Viljujsky District of the Yakut Area. St. Petersburg, Russia *in* 1994 edition: Viljujsky District of the Yakut Area. Yana Publishing House, Moscow, Russia. (In Russian).

Markgren, G. 1974. The moose in Fennoscandia. Canadian Naturalist 101: 185-194.

Markov, G. G., and A. A. Danilkin. 1996. Kraniometricheskaja in Eurasia (The characteristics of moose in Eurasia). Russian Academy of Sciences, Biological Series P: 244-247. Moscow, Russia. (In Russian).

Menzbir, M. 1878. Characteristics of distribution of animals. Nature and Hunting 10: 32-34. Moscow, Russia. (In Russian).

Michurin, L. N., and O. N. Mironenko. 1967. About moose in the Putorano mountains. Pages 72-75 *in* Biology and Economy of the Moose. Rosselhozizdat, Moscow, Russia. (In Russian).

Middendorf, A. 1869. Travel in northern and eastern Siberia by Siberian fauna. 2(5) St. Petersburg, Russia. (In Russian).

Nasimovich, A. A. 1955. The Role of Snow Cover in the Lives of Ungulates in the USSR. Publishing House of the Academy of Sciences of USSR, Moscow, Russia. (In Russian).

Naumov, H. П. 1934. Mammals of the Tungus District. Work of the Polar Commission. Publishing House of the Academy of Sciences of USSR, Moscow, Russia. (In Russian).

Nygrén, K., P. Danilov, and T. Nugren. 2008.

The dynamics and management of North European moose. 6th International Moose Symposium. Yakutsk, Russia, 14-20 August, 2008. Abstract only.

Obermeier, G. 1913. The Prehistoric Person. Translated from German, P.J. Schmidt. Edition of Brockhaus and Efron, St. Petersburg, Russia. (In Russian).

Oshanin, A. 1934. Trade and sports hunting from northern Manchuria. Collection of Works 7: 12-24. Moscow, Russia. (In Russian).

Panov, N. K. 1999. History of development of vegetation of a mountain part of the Southern Urals Mountains in the late Pleistocene and Holocene, on paleontological data. Pages 144-158 *in* N. G., Smirnova, editor. Historical Ecology of Animals in the Southern Ural Mountains. Sverdlovsk, Russia. (In Russian).

Preobrazhenskiy, V. S. 1960. Kodarskiy glacial region (Trans-Baikal). Ninth Scetion of IGY Program (glaciology). No. 4. Publishing House of the Academy of Sciences of USSR, Moscow, Russia. (In Russian).

Rakov, N. V. 1964. Geography and ecology of moose populations in Amur-Ussurijskij kraj. Pages 44-100 *in* Biology and Economy of the Moose. Rosselhozizdat, Moscow, Russia. (In Russian).

_____. 1965. Distribution and ecology of moose in Amur-Ussurijskij kraj. Pages 28-65 *in* Biology and Economy of the Moose. Rosselhozizdat, Moscow, Russia. (In Russian).

Rozhkov, J. I., A. V. Pronjaev, O. V. Piskunov, N. E. Ovsjukova, A. V. Davydov, and L. V. Rozhkova. 2001. Moose. The population-biological analysis of license information. Hunting Russian Animals. Issue 4. Tsentrohotkontrol, Moscow, Russia. (In Russian).

_____, _____, _____, _____, _____, and _____. 2002. Moose of the European part of the Russian Federation. Population division, selection, seasonal changes, morphological, and ethological differentiation (by results of the analysis of the license information). Pages 153-158 *in* Questions For Modern Game Biologists. Tsentrohotkontrol, Moscow, Russia. (In Russian).

Sablina, T. B. 1955. Ungulate Belovezhskoi Pushi. Page 15 *in* A. N. Severtsova, editor. Works of the Institute of Morphology and Ecology of Animals. Moscow, Russia. (In Russian).

Safronov, V. M. 2009. Regional populations and migration of moose in northern Yakutia, Russia. Alces 45: 17-20.

Semenov-Tjan-Shanskij, O. I. 1948. Moose on the Kola Peninsula. Works of the Lappish Reserve 2: 91-162. Moscow, Russia. (In Russian).

Serzhanin, I. N. 1961. Mammals of Belarus. Minsk Publishing House, Izdatelstvo Akademii Nauk, Belorusskoi SSR, Minsk, Russia. (In Russian).

Severtsev, N. A. 1854. Moose or sohatii. Bulletin of Natural Sciences 19: 290-299.

Sipko T. P., V. I. Fil, and A. R. Gruzdev. 2004. Resettlement of moose. The Siberian Zoological Conference, Novosibirsk, Russia, 15-22 September, 2004. Abstract only.

_____, _____, and _____. 2008. Moving moose on Kamchatka. 6th International Moose Symposium, Yakutsk, Russia, 14-20 August, 2008. Abstract only.

Skalon, V. N., I. Scherbakov, and M. Bazikin. 1941. Nature and Socialist Facilities. Volume 8. Moscow, Russia. (In Russian).

Sludsky, A. A. 1953. Eviction of "taiga" animals in the forest-steppe and steppes of Western Siberia and Kazakhstan. The Nature Branch of Biology 53 (2): 14-32. Moscow, Russia. (In Russian).

Sobansky, G. G. 1975. Territorial accommodation of ungulates in the Altay mountains. Pages 122-123 *in* Ungulate Fauna of the USSR. Moscow, Russia. (In Russian).

_____. 1992. Ungulates in the Altai Mountains. Novosibirsk, Russia. (In Russian).

Sokolov, I. I. 1959. Ungulates (Perissodactyla and Artiodactyla). *In* Fauna of the USSR. Mammals. Nauka Publishing House, Moscow, Russia. (In Russian).

Tavrovsky, V. A., O. V. Egorov, and V. G. Krivosheev. 1971. Mammals of Yakutia. Nauka, Moscow, Russia. (In Russian).

Tikhonov, A. N. 1990. History and systematization moose. 3rd International Moose Symposium. Syktyvkar, Russia, 27 August-5 September. Abstract only.

Timofeeva, E. K. 1974. Moose: Ecology, Distribution, and Economic Importance. Leningrad University Publishing House, Leningrad, Russia. (In Russian).

Vereshchagin, N. K. 1967. The geological history of moose and its relationship to man. Pages 3-37 *in* Biology and Economy of the Moose. Rosselhozizdat, Moscow, Russia. (In Russian).

_____, and A. Nikolaev И. 1979. Trade animals of Neolith tribes of Kamchatka. The Nature Branch of Biology 84 (5): 40-44. Moscow, Russia. (In Russian).

_____, and O. S. Rusakov. 1979. Ungulates from the North-Western Part of the USSR. Nauka, Leningrad, Russia. (In Russian).

Woillard, G. 1979. Abrupt end of the last interglacial in north east France. Nature 281 No. 5732: 558-562.

Yanushevich, A. I. 1952. Vertebrate Fauna of the Tuva Area. Zap-Sib Publishing House, Novosibirsk, Russia. (In Russian).

Yazan, J. P. 1966. Moose in the northern Caucasus. The Nature Branch of Biology 71 (4): 123-125. Moscow, Russia. (In Russian).

Yurlov, K. T. 1965. Change in moose range in the southern West-Siberian lowlands. Pages 17-27 *in* Biology and Economy of the Moose. Rosselhozizdat, Moscow, Russia. (In Russian).

Zheleznov, N. K. 1990. Wild ungulates in northeastern USSR. Vladivostok, Russia. (In Russian).

Zhen Zuoxin. 1956. Animals and birds of China. The Nature Journal 10: 3-18. Moscow, Russia. (In Russian).

Zhitkov, B. M. 1914. Moose in Ussurijskogo Kraj. Zoological Branch of Natural Sciences: A New Series 2 (3): 5-14. St. Petersburg, Russia. (In Russian).