A REVIEW OF CIRCUMPOLAR MOOSE POPULATIONS WITH EMPHASIS ON EURASIAN MOOSE DISTRIBUTIONS AND DENSITIES

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ABSTRACT: Moose (*Alces alces)* may be among one of the most susceptible big game species to climate change. Development of long-term circumpolar databases of this species' densities and distributions, combined with biological, ecological, and management-related metrics, can help guide research and future international management strategies. We emulated methodology previously used to summarize North American moose population and harvest densities for Eurasian countries with free-ranging moose populations. From these data, we created a GIS layer that summarized the circumpolar distribution and density of moose. The following summary analysis of these data indicates that moose have both expanded and contracted along their southern range boundary in recent decades – with losses along the southern range in eastern Asia, particularly China, Mongolia, and Kazakhstan. In contrast, we documented distributional gains along the western and southwestern range in Europe (Poland, Germany, Czech Republic, Slovakia). In total, 21 countries have free-ranging moose populations; 8 with sustainable populations and hunting seasons, 5 with sustainable populations but no hunting season, and 8 with vagrant individuals occasionally sighted. A region of high-density moose populations spans from the Scandinavian and Baltic countries into the Russian oblasts of Perm and Sverdlovsk. Distributions ca. 2010 indicated that moose occupied an area of about 16,712,600 km^2 in Eurasia. Primary range (management units with ≥0.11 moose per km^2) composed only 18% of the occupied range while supporting more than 66% of the estimated 1.2 million moose in Eurasia. Additionally, 47% (149,860) of the moose harvested were taken on 10% (1,722,660 km^2) of the range. The 2010 circumpolar moose population was estimated to be more than 2.2 million and occupied a range of 26,205,000 km^2. Time-series analyses can offer a simple and cost-effective approach to monitor the status of moose populations across large geographical regions and might be particularly insightful given the current and predicted future influences of climate change on moose. Other analyses might address population dynamics, habitat, environmental constraints, and harvest management, among other issues. We encourage jurisdictions to cooperate strategically in implementing and coordinating GIS analyses to monitor, assess, and manage moose populations around the world. We believe these maps can serve as a useful tool for educating the public and policy makers about the importance of habitat and land use practices with respect to maintaining sustainable populations of moose and other species that are dependent upon boreal, temperate broadleaf, and mixed forests.

ALCES VOL. 56: 63–78 (2020)

Key Words: *Alces alces*, Asia, distribution, Eurasian elk, Europe, GIS, harvest, moose, population density

Peterson (1955) provided a map showing the general circumpolar range distribution of moose (*Alces alces*). The most recent attempt to map circumpolar moose populations in both Eurasia and North America of which we are aware was by Telfer (1984) who also provided circumpolar estimates of probable southern range limits of *Alces* spp. during Wisconsin glaciation (10,000 years ago), and extirpations of moose from their historic ranges in Europe since Roman times (2,000 years ago) and in North America since the 1600s. Gill (1990) reviewed moose distributions and population numbers for North America and Europe but lacked information about Russian and Asian moose populations. Nowak (1999) later estimated there were ~900,000 moose in North America and 1 million in Eurasia. Apollonio et al. (2010) updated information for central European moose populations, but again lacked information for eastern European and Asian moose. All the while, numerous changes regarding range expansion and contraction occurred in the 30-year period of 1980–2010, particularly along the southern range boundary of moose.

Jensen et al. (2018) summarized the North American range distribution and densities of moose for the years circa 2010. The objective of this project was to assimilate data for moose into GIS layers for Eurasian moose populations that were compatible with Jensen et al. (2018), thus providing a circumpolar distribution map for moose. Here, we present a series of maps and enumerate patterns observed in the circumpolar distributions and densities of moose. We are optimistic that our effort will help researchers identify areas of concern and help address moose management issues that cross political boundaries.

METHODS

We contacted wildlife professionals in each European and Asian country (Table 1) with free-ranging populations of moose to obtain population estimates and harvest rates by management unit for the year 2010 or the closest year. Either a representative wildlife professional from the country provided data directly into our electronic spreadsheet, or we entered data from available literature sources when unable to establish a professional contact; all data were double-checked for accuracy.

The size and scale of management units, as well as methods for determining population estimates varied by jurisdiction (e.g., various survey methods, statistical software packages, and license sales). Where GIS data were unavailable, management unit boundaries were digitized (ArcGIS ArcMap 10.4.1, ESRI, Inc., Redland, California, USA) from available paper maps. When jurisdictions did not have management units or hunting seasons, we used political, jurisdictional boundaries to delineate surrogate

Table 1. A summary of information sources obtained for GIS mapping of circumpolar moose range distribution and densities in 2010. Bolded names indicate personal communication.

Country	Information Source
Austria	**Klaus Hackländer**, Institute of Wildlife Biology and Game Management, Gregor-Mendel-Strasse 33, 1180 Vienna, Austria
Belarus	**Alexander Kazarez**, Dept. of Hunting Science, Belarus State Technological University, Minsk, Republic of Belarus
China (Peoples Republic)	**Heng Bao** and **Guangshun Jiang**, Feline Research Center of Chinese State Forestry Administration, College of Wildlife and Protected Areas, Northeast Forestry University, 26 Hexing Road, Harbin 150040, China
Croatia	Hundtermark (2016)
Czech Republic	Homolka (1998)
Estonia	**Rauno Veeroja**, Nature Department, Estonian Environment Agency, Tartu
Finland	**Jyrki Pusenius**, Finnish Game and Fisheries Research Institute, Joensuu, Finland
Germany	**Marco Heurich,** University of Freiburg, Freiburg, Germany
Hungary	**Sandor Csányi**, Szent István University, Institute for Wildlife Conservation, Gödöllő, Hungary
Kazakhstan	Hundtermark (2016)
Latvia	**Gundega Done,** LSFRI "Silava," Salaspils, Latvia
Lithuania	**Linas Balciauskas**, Nature Research Centre, Akademijos 2, 08412 Vilnius, Lithuania
Moldova	Volokh (2009)
Mongolia	Clark et al. (2006)
Norway	**Erling Solberg,** Norwegian Institute for Nature Research, Trondheim, Norway
Poland	Bank Danych Lokalnych (BDL), Statistics Poland
Romania	**Gabriel Chisamera** and **Dumitru Murariu,** Travaux Museum of Natural History, Hundtermark (2016), Mitchell-Jones et al. (1999)
Russia	Lomanova et al. (2011)
Slovakia	**Stanislav Bystiansky** and **Zuzana Chovanova,** Technical University of Zvolen, Slovakia
Sweden	**Fredrik Widemo,** Swedish University of Agricultural Science, Umea, Sweden
Ukraine	Volokh (2009)

spatial units. We then calculated moose population and harvest densities (per km^2) for each management unit. Density estimates within each management unit were made under the assumption that animals were evenly and randomly distributed. Attribute information associated with each data record included: source of information, unit name or identification number, unit area (km^2), and "reliability" of the data. Reliability of population estimates ranged from "best guess" to statistically valid, systematic surveys. Estimates of hunter harvest varied with respect to whether they included or excluded categories of subsistence hunting. We collected moose distribution and density data from survey and harvest records collected at the management unit scale (n = 761) for the years closest to 2010 using the same approach as Jensen et al. (2018). We compiled these data from agency and university personnel responsible for managing lands with free-ranging moose populations. We relied upon available data in the literature if appropriate contacts were unavailable.

We followed the procedures used by Jensen et al. (2018) to produce a circumpolar map of range distribution and density of moose. We ranked management units by density and categorized them into 5 ordinal groups of equal unit counts for display purposes. We then estimated two characterizations of primary range for each decade by selecting only geographical units with values at or above the 50th percentile for population and harvest density. We then divided this 50th percentile subset into 5 groups of equal unit counts to display variation in density (Jensen et al. 2018). All maps produced here use the same ordinal groups as in Jensen et al. (2018).

RESULTS

There were disparities in methodology, types of data, and quality of information available, yet broad patterns emerged when summarizing circumpolar moose distributions. GIS layers from Belarus, Estonia, Finland, Latvia, Norway, Russia, and Sweden were digitized directly by agency personnel, while we entered layers for the remainder of jurisdictions based on available reports and/or publications. Individual moose management units, when available, were mapped for all 17 countries with free-ranging populations. We did not map 4 countries (Croatia, Hungary, Moldovia, Romania) with rare occurrences of vagrant moose. A total of 761 units with moose population estimates were mapped with intensity and scale of monitoring highly varied by country. For example, Norway manages 426 units representing ~2% of the total moose range, whereas Russia provided information from 68 political jurisdictions representing ~82% of the total moose range. The following summaries provide information by country. Summary maps and harvest table are provided within and addressed specifically in the Discussion.

Austria

Moose have immigrated infrequently from core areas in the Czech Republic since 1964. Observations have increased, especially in the area of Waldviertel (Lower Austria) and Mühlviertel (Upper Austria) and as far south as the Danube River near Vienna, since the collapse of the Soviet Union and the relaxation of barriers between

Fig. 1. Current moose range in northeast China (Ma et al. 2020).

eastern and western Europe (1991). Many of these moose have perished in vehicular collisions or were legally shot (Bauer and Spitzenberger 2001). Although moose are observed every year in Austria, no resident population has been established to date.

Belarus

We obtained distribution, population, and harvest densities from Alexander Kazarez (Dept. of Hunting Science, Belarus State Technological University, Minsk, Belarus). In 2010, moose were found in all 6 oblasts at an overall density of 0.12 moose/km^2, and 0.33 moose/km^2 in moose habitat specifically; highest densities were in the northern oblast of Vitebsk (0.20 moose/ km^2 oblast-wide and 0.56 moose/km^2 in moose habitat). Harvest density in moose habitat was 0.03 moose/km^2 in 2010. The estimated 2010 population was 24,300 animals with a harvest of 1,886 animals; population estimates are constructed post-harvest.

China (Peoples Republic of)

We derived the current range distribution of moose from Ma et al. (2020) (Fig. 1). Renzhu et al. (1993) estimated that 7,000 moose occupied the Greater Khingan Mountains and another 3,000 inhabited the Lesser Khingan Mountains (ca. 1990). Zhi et al. (2014) reported that ~ 3,015 (ca. 2008) and 2,648 (ca. 2014) moose occupied the Greater Khingan Mountains of Inner Mongolia. In 2012–2015, Bao et al. (2017) estimated population densities of 0.75 moose/km^2 in Hanma (73 km^2), 0.4 moose/km^2 in Shuanghe (73 km^2), 0.24 moose/km^2 in Nanwenghe (198 km^2), 0.16 moose/km^2 in Meitian (92 km^2), 0.08 moose/km^2 in Mohe (213 km^2), and 0.1 moose/km^2 in Zhanhe (197 km^2); Hanma and Meitian are in the Greater Khingan Mountains of Inner Mongolia. Shuanghe, Nanwenghe, and Mohe are part of the Greater Khingan Mountains, and Zhanhe is part of the Lesser Khingan Mountains of Heilongjiang Province (Fig. 1). Moose are classified as first-class protected animals with all hunting prohibited. An increase in late spring temperatures may shift the southern distribution northwards in the Heilongjiang province (Dou et al. 2013).

Croatia

Hundtermark (2016) reported vagrant moose in Croatia. The nearest countries with established moose populations are the Czech Republic (525 km to the north) and the Ukraine (600 km to the northeast).

Czech Republic

Since 1993, a small population averaging 28 moose has straddled the borders of the Czech Republic, Austria, and Germany (Romportl et al. 2017). Moose were found in two core areas until recently. The population in the eastern part of Třeboň was extirpated during the first decade of the 21st century. The second is south and west of Lipno Dam in an area ~100 km^2 (Anděra and Červený 2009) and ~200 km from more stable populations in Poland to the northeast (Homolka 1998, Bartos et al. 2010). Occasional sightings of vagrant moose occur outside these areas, particularly along the Polish border (Homolka 1998, Bartos et al. 2010).

Estonia

We obtained distribution, population, and harvest densities from Rauno Veeroja (Nature Department, Estonian Environment Agency, Tartu, Estonia). Moose are found in all 15 Estonian counties ranging in density from 0.2 to 0.6 moose/km^2; highest densities occur in Harju and Parnu Counties. Harvest density ranges from 0.05 to 0.17 moose/km^2; highest harvest occurs in Harju, Laane, and Parnu Counties. The 2010 post-hunt population was estimated as 14,700 after harvest of 4,255 animals.

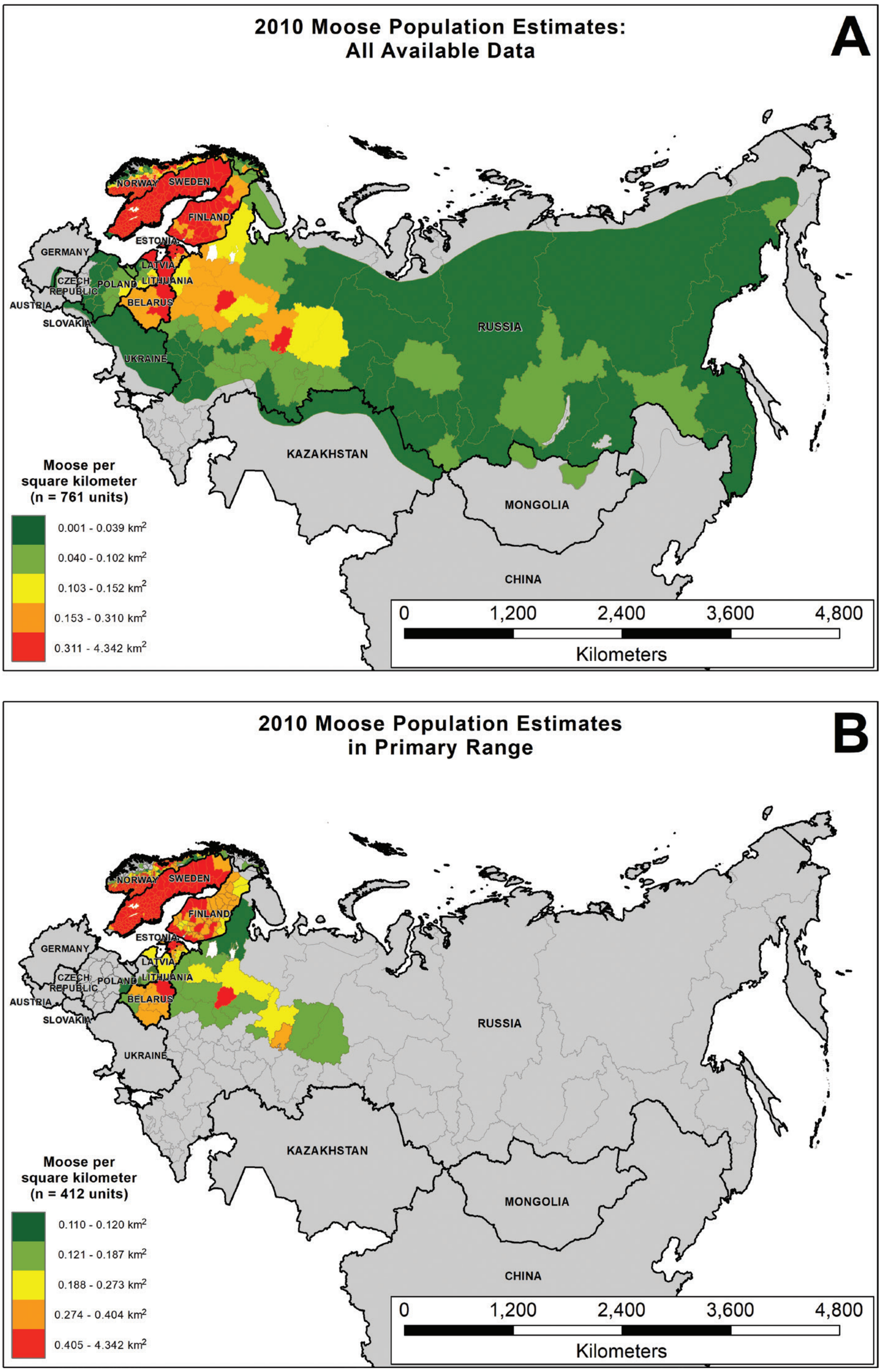

Fig. 2. Moose population density estimates, by management unit, for Eurasia (ca. 2010). Panel A represents all available management unit data (n = 761). Panel B represents moose population density estimates for management units considered as primary range (defined as densities ≥0.11 moose/km^2; n = 516 units) with the highest population densities.

Table 2. Eurasian moose summary of post-harvest populations and annual harvest estimates by country for 2010 or closest year. V = Vagrant population. N/A = not applicable for countries without hunting seasons.

Countries	Post Harvest Population Estimate (ca.2010)	Annual Harvest (ca. 2010) [% of Pre-Harvest Pop.]	Area (km^2)
Austria[1,2]	V	N/A	5,200
Belarus[3]	24,300	1,886 [8%]	414,600
Czechia[2,4]	<50a	N/A	8,400
China[5]	2,650[a]	N/A	88,500
Croatia[6,7]	V	N/A	
Estonia[8]	14,700	4,255 [29%]	43,900
Finland[9]	95,800	68,430 [42%]	330,000
Germany[2]	V	N/A	10,000
Hungary[6]	V	N/A	
Kazakstan[6]	V	N/A	441,200
Latvia[10]	16,400	2,858 [17%]	64,600
Lithuania[11]	6,560	198 [3%]	65,000
Mongolia[12]	10,000[a]	N/A	152,500
Moldova[6]	V	N/A	
Norway[13]	107,400	36,107 [25%]	282,400
Poland[14]	7,550[a]	N/A	269,200
Romania[6, 7, 15]	V	N/A	
Russia[16]	657,000	19,882 [3%]	13,644,000
Slovakia[17]	V	N/A	26,900
Sweden[18]	265,000	98,000 [27%]	438,100
Ukraine[19]	4,500[a]	N/A	428,100
Total	1,211,910	231,616	16,712,600

[1]Klaus Hackländer (pers. comm.), [2]Marco Heurich (pers. comm.), [3]Alexander Kazarez, (pers. comm.), [4]Homolka (1998), [5]Hen Bao and Guangshun Jiang (pers. comm.), [6]Hundtermark (2016), [7]Wilson and Mittermeier (2011), [8]Rauno Veeroja (pers. comm.), [9]Jyrki Pursenius (pers. comm.), [10]Gundega Done (pers. comm.), [11] Linas Balciauskas (pers. comm.), [12]Clark et al. (2006), [13]Erling Solberg (pers. comm.), [14]Bank Danych Lokalnych (BDL), Statistics Poland, download from https://bdl.stat.gov.pl/BDL/, [15]Mitchell-Jones et al. (1999), [16]Lomanova et al. (2011), [17]Zuzana Chovanova and Stanislav Bystiansky (pers. comm.), [18]Fredrik Widemo (pers. comm.), [19]Volokh (2009).
[a]No hunting season.

Finland

We obtained distribution, population, and harvest densities from Jyrki Pusenius (Finnish Game and Fisheries Research Institute, Joensuu, Finland). Moose are managed in 60 management areas with density ranging from 0.05 to 1.5 moose/km^2. The highest regional density occurs in the southern third of the country in Inland Finland (Lavsund et al. 2003), whereas highest local densities are in management units in the Coastal Finland region. Harvest density in management areas ranges from 0.01 to 0.45 moose/km^2; population estimates are constructed post-harvest.

Germany

A small population of 10 to 20 moose straddle the border regions of Austria, Czech Republic, and Germany (Romportl et al. 2017). These animals are mostly located in the Czech Republic, but occasionally both sexes are sighted in the state of Bavaria, mostly in

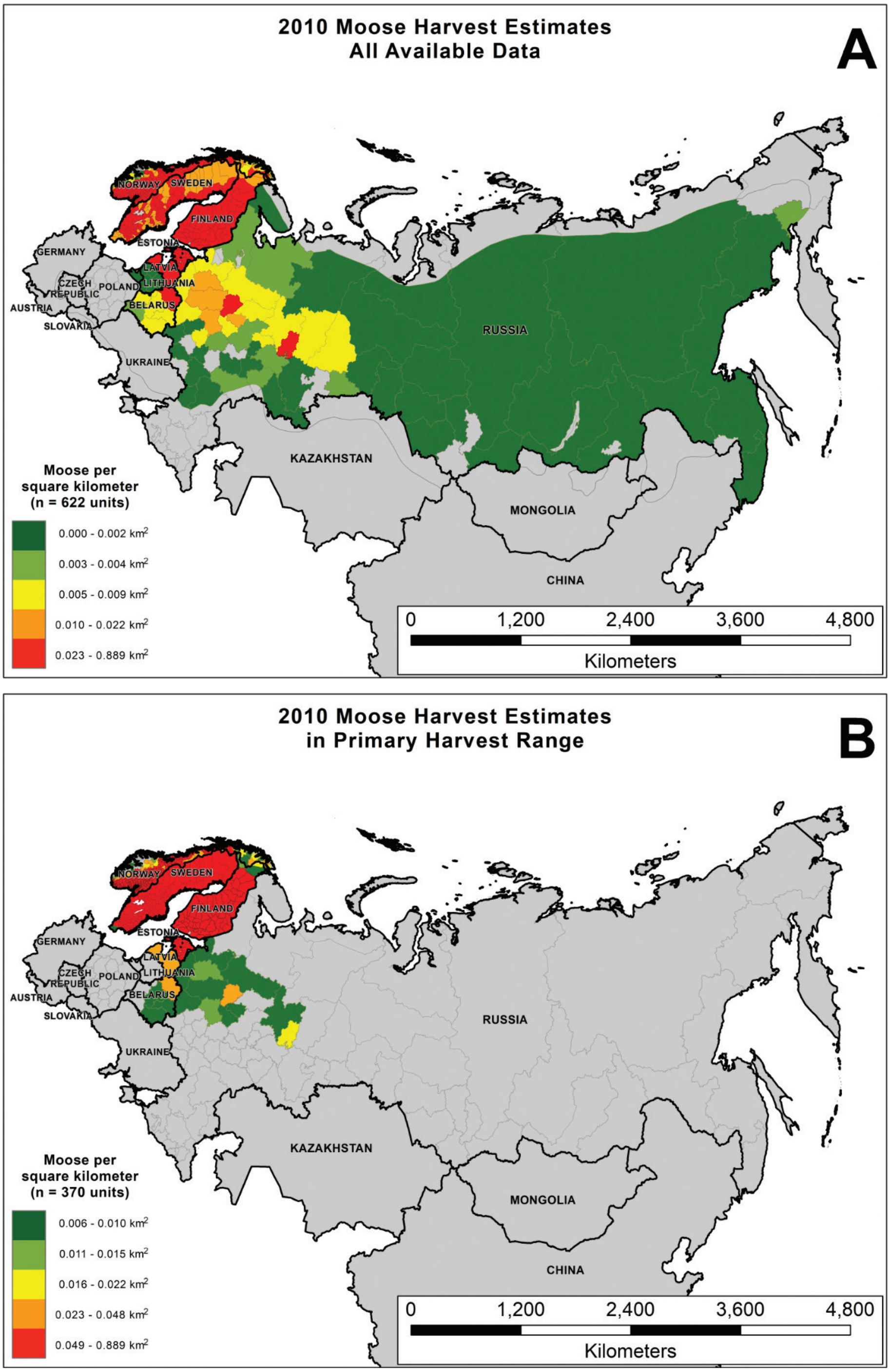

Fig. 3. Moose harvest density estimates, by management unit, for Eurasia (ca. 2010). Panel A represents all available management unit data (n = 622). Panel B represents moose harvest density estimates, by management unit, for the units considered to be primary range (defined as densities ≥0.006 moose/km^2) (n = 370 units) of the management units with the highest harvest densities.

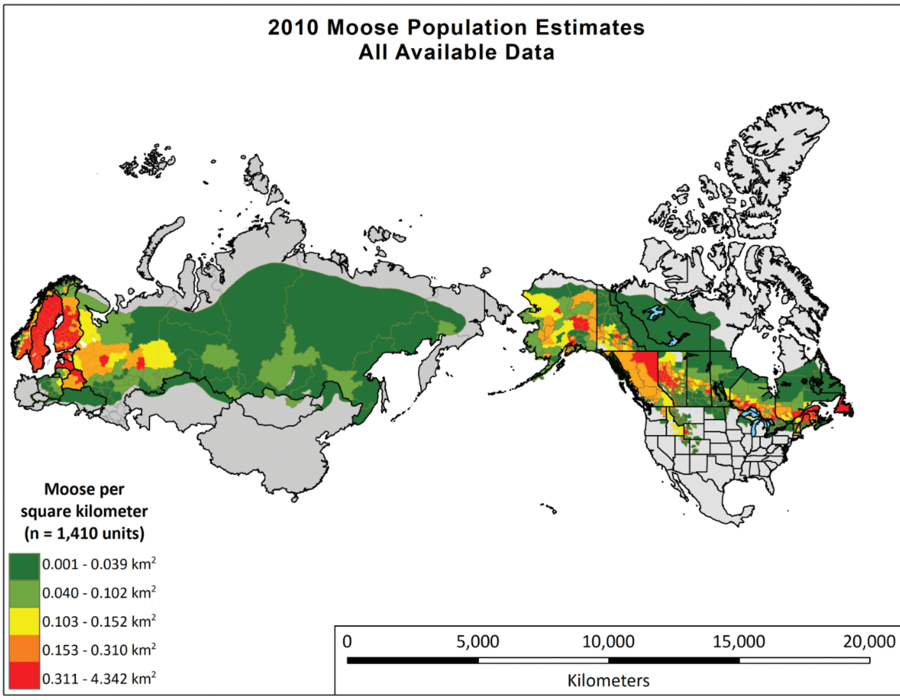

Fig. 4. Circumpolar moose population density estimates, by management unit, for all available management units (ca. 2010) (n = 1,410 units). North American range map from Jensen et al. (2018).

the counties of Regen and Freyung-Grafenau (Marco Heurich, University of Freiburg). More recently, young males were sighted increasingly in Eastern Germany (State of Brandenburg, Mecklenburg-Vorpommern, Saxony) along the Polish border. In 2012, a moose was hit and killed on highway A10 a few km outside Berlin (www.spiegel.de/international/germany/wild-elk-returns-to-germany-a-853581.html).

Hungary

Hundtermark (2016) reported vagrant moose in Hungary. Sándor Csányi (Szent István University, Gödöllő, Hungary) observed that: "… sporadic observation [of moose] can be found in the hunting/zoological literature but these are rare and many of them never confirmed. As far as I remember, a young bull was shot in the late 1980s or the first part of the 1990s but since that time no moose was reported. Generally speaking, Hungary is far south of [the] current range of moose and even dispersing individuals have a low chance of reach[ing] our forest." Anecdotally, Homonnay (1985) mentioned 4 moose living in northeast Hungary at the end of the 1970s and unconfirmed observations of a cow in the central parts of the country. According to other sources, these 4 moose escaped from confinement at a former Soviet military base (Faragó 2002).

Kazakhstan

Hundtermark (2016) reported moose in Kazakhstan but we were unable to find any current information; however, Heptner et al. (1988) included the northern border of Kazakhstan within the southern range of moose. Likewise, we used Heptner et al. (1988) to delineate a portion of the southern range distribution in Asia. We assumed the population was minimal and that moose were not hunted within a range of 44,200 km^2. We estimated a population of 50 individuals and density of 0.001 moose/km^2.

Latvia

We obtained distribution, population, and harvest densities from Gundega Done (LSFRI "Silava," Salaspils, Latvia). Moose are found throughout Latvia with an overall density of 0.25 moose/km^2; highest densities tend to occur in the northeastern region (Andersone-Lilley et al. 2010). Overall harvest density in 2010 was 0.04 moose/ km^2. In 2010, the population was estimated as 16,400 with a harvest of 2,858 animals; population estimates are constructed post-harvest.

Lithuania

We obtained distribution, population, and harvest densities from Linas Balciauskas (Nature Research Centre, Vilnius, Lithuania). Moose are found throughout Lithuania with an overall density of 0.10 moose/km^2; highest densities occur in the district of Zarasai (0.27 moose/km^2) in the northeastern region. In 2010, harvest density was 0.003 moose/ km^2 overall, and 0.03 moose/km^2 (n = 33) in the district of Zarasai. Population estimates are constructed pre-harvest.

Moldova

Volokh (2009) mapped observations and small pockets of moose in central Moldova. We assumed vagrant moose from the Ukraine occasionally wander into Moldova.

Mongolia

Clark et al. (2006) reported moose (*A. a. cameloides*) in the Nomrog River Basin of eastern Mongolia along the Chinese border, and in the Henitii and Hangai mountain ranges in north-central Mongolia (*A. a. pfizenmayeri*). The population estimate in the Henitii and Hangai mountains was 10,000 animals in 1989, whereas in the Nomrog Strictly Protected Area in the Ikh Hyangan Mountains Range moose are rare, with only 73 animals sighted in 2004 (Clark et al. 2006).

Norway

We obtained distribution, population, and harvest densities from Erling J. Solberg (Norwegian Institute for Nature Research, Trondheim, Norway). Moose are managed in 426 management areas with density ranging from <0.01 to 2.5 moose/km^2; highest densities are in Hedmark (1.0 moose/km^2) and Ostfold Counties (0.95 moose/km^2) in southeastern Norway near the Swedish border (Lavsund et al. 2003). In 2010, Norway estimated their total population as 107,400 and harvested 36,107 animals; harvest density ranged from <0.01 to 0.89 moose/km^2. Population estimates are made post-harvest.

Poland

We obtained distribution, population, and harvest densities from Bank Danych Lokalnych, Statistics Poland; (https://bdl.stat.gov.pl/BDL/). Moose were reported in 13 of 16 provinces in 2010; none occurred in Lubuskie, Dolnoslaskie, and Opolskie Provinces along the German and Czech Republic border. Density was highest (0.1 moose/km^2) in Podlaskie Province along the Belarus and Lithuania borders. The 2010 population estimate was 7,550 animals with an average density of 0.03 moose/km^2. The 2010 average harvest density was <0.001 moose/km^2 (n = 24 animals).

Romania

Mitchell-Jones et al. (1999) reported moose in the Carpathian Mountains of

Suceava County, an area <400 km from a stable moose population in the Ukraine (Volokh 2009). Hundtermark (2016) reported vagrant moose in Romania and we likewise assumed that moose occasionally wander into Romania from the Ukraine population.

Russia

We obtained distribution, densities, and harvest rates in Russia and the exclave of Kaliningrad (Lomanova et al. 2011). Moose were reported in all 68 krai, oblasts, and republics that lay within moose range. Range boundaries generally followed those provided by Heptner et al. (1988) and closely mimic those described by Makarova and Khokhlov (2009), Minoranskiy et al. (2009), and Safronov (2009). It should be noted that in larger oblasts of eastern Russia, the boundaries we present do not account for gaps in moose range due to terrain and distinct populations (Safronov 2009); therefore, densities were probably underestimated within these eastern political jurisdictions. Population density ranged from <0.01 to 0.5 moose/km^2 with highest densities in western Russia, particularly in the oblast of Yaroslavl and Udmurt Republic. Harvest density ranged from <0.001 to 0.037 moose/km^2. Population estimates are constructed post-harvest.

Slovakia

Mitchell-Jones et al. (1999) indicated that moose were present in the Fatra and Carpathian Mountains along the Polish border. Zuzana Chovanova and Stanislav Bystriansky (Technical University of Zvolen, Slovakia) reported sporadic sightings of moose since 1960 in the regions of Banska Bystrica, Košice, Nitra, Presov, Trnava, and Zilina along the border of Ukraine, Poland, and the Czech Republic. Given that there are <20 animals, we assumed that sightings are vagrant animals from neighboring countries and that no reproducing population exists.

Sweden

We obtained distribution, population, and harvest densities from Fredrik Widemo (Swedish University of Agricultural Science, Umea, Sweden). Moose are managed in 148 management areas with a national average density prior to hunting of 0.84 moose/km^2. The average harvest is of 0.23 moose/km^2 ranging from 0.09 to 0.45 moose/km^2; the annual harvest rate is ~27%. Based on this rate, the estimated population density ranged from 0.33 to 1.67 moose /km^2. Highest densities were found in the Southern Norrland, Southern Götaland, and Western Götaland regions along the Norwegian border (Lavsund et al. 2003). Based upon the 2010 harvest of ~98,000 moose, we estimated the total population as ~265,000 animals post-harvest; however, population estimates are typically constructed pre-harvest.

Ukraine

We derived the range distribution and population estimates from Volokh (2009) who estimated that the 2003 population was 4,500 moose with a density ~0.01 moose/km^2. Hunting is prohibited in the Ukraine (Volokh 2009).

Miscellaneous refuge moose populations

In 1910 an effort was made to establish a free-ranging moose population in New Zealand when 4 males and 6 females (2 died shortly after release) were released in Dusky Sound. It is generally accepted that this translocated population was extirpated by the 1950s (Nugent et al. 2001). Outside of zoological gardens, we know of moose held in 2 refuges behind high fences in Scotland and Denmark. A pair of moose were translocated from Sweden in 2008 and released into a 9,300 ha fenced reserve on the Alladale estate north of Inverness, Scotland to establish a breeding population (https://www.countrylife.co.uk/news/country-life-today-may-31-2019-197056). Five moose were translocated from Sweden in 2016 and released into a 21 km^2 fenced area at Lille Vildmose in eastern Himmerland, Denmark (Mads Frost Bertelsen, Dept. of Veterinary and Animal Sciences, University of Copenhagen; pers. comm.).

DISCUSSION

Piecing together population and harvest density estimates from multiple countries is inherently problematic; however, patterns emerge when viewed at the landscape scale. As in North America, moose density along the northern range boundary appears low but relatively stable, although harvest densities were well below 0.01 moose/km^2. More recently, increasing moose density at these latitudes and in shrub habitat in the Canadian high arctic have been linked to climate change (Tape et al. 2016), and this same pattern may be occurring in Eurasia. Moose distribution across the southern Eurasian range extends south in the mountainous regions of the Ukraine, Russia, Kazakhstan, Mongolia, and China (Fig. 2a). This pattern of moose extending their range into higher elevations at southern latitudes has also occurred in North America along the Rocky Mountains (Jensen et al. 2018). Conversely, Dou et al. (2013) suggest that an increase in late spring temperatures may shift the southern range limit of moose northward in Heilongjiang Province in China, and this may be occurring in other areas along the southern range border.

Telfer (1984) wrote that "… vast subarctic areas with substantial mountain tundra and taiga areas show average regional densities of less than 0.1 moose/km^2. Better boreal and coniferous/deciduous transition ranges support regional averages of 0.1 to 0.3 moose/km^2 while excellent range in those areas with deciduous vegetation and soft, thin snow covers average 0.4 to 1.0 moose/km^2."

In 2010, the highest moose densities and harvest rates in Eurasia were found within primary range (defined as densities ≥ 0.11 moose/km^2) in Fennoscandia, Baltic countries (Estonia, Latvia, Lithuania), eastern Poland, Belarus, and western Russia (Fig. 2a, 2b, 3a, 3b). This region is dominated by boreal and temperate broadleaf and mixed forest (Olsen et al. 2001). In 2010, Eurasian moose range encompassed a total area of ~16,712,600 km^2, with ~82% of that range in Russia. However, a relatively small region of primary range (~3,065,400 km^2), <18% of the total moose range, supports ~803,700 moose or >66% of the Eurasian moose population. In comparison, North American moose range encompassed an area of >9,492,400 km^2 in 2010; however, a narrow band of primary range of 803,400 km^2, or just 30% of the total range, supported >890,700 moose or ~89% of the total population (Jensen et al. 2018).

Combined with the North American population of 1.0 million moose occupying a range of 9,492,400 km^2, the circumpolar moose population in 2010 was estimated as ~2,212,000 animals with a range distribution of >26,205,000 km^2. From a circumpolar view, the primary range accounts for only 22% of the total occupied range yet supports 77% of the world's moose population. Not surprisingly, a similar pattern exists with harvest data in Eurasia where 149,860 moose (47% of the total harvest) were harvested on 1,722,700 km^2 or 10% of the primary range.

The highest moose population densities in the world appear to be in Fennoscandia. Intensive forest management and optimizing harvest rates appear to be the driving factors for high densities in the region (Dettki et al. 2003). Within this region is a pattern of moose reaching highest densities in the coastal management units of Estonia, Finland, Norway, and Sweden. Similar patterns of high densities occur in North American along the northern shoreline of the Great Lakes, maritime provinces, and coastal region of Quebec (Jensen et al. 2018). Dettki et al. (2003) reported that "… altitude seemed to be the single most important factor, separating the high HSI [Habitat Suitability Index] values along the coastal lowlands from the lower HSI values in the inland at a generally higher altitude." The moderating influences of oceans and large water bodies on weather conditions, particularly on snow depth (Renecker and Schwarz 1998), may influence feeding and habitat use at the landscape scale.

This three-fold increase in population density in primary versus secondary moose range emphasizes the importance of habitat as a driver for moose populations. That said, unrelated anthropogenic factors such as political instability (Bragina et al. 2015) and poaching (Glushkov 2009, Kuhl et al. 2009, Braden 2014), as well as dramatic increases in predator numbers (Bragina at al. 2015), can dramatically influence large mammal populations. For example, moose abundance in post-Soviet countries are several times lower than in Scandinavia (Table 2). Additionally, what might be considered generally as secondary moose range may be critical habitat for subspecies of moose struggling for survival as with *A. a. cameloides* in Mongolia and the Peoples Republic of China (Clark et al. 2006). Moose populations in China and Mongolia appear to have declined significantly in recent decades despite protection from hunting (Renzhu et al. 1993, Zhi et al. 2014).

A review of circumpolar moose distribution and relative density maps (combined maps from this project and Jensen et al. 2018, Fig. 4) confirm several key points raised by Karns (1998) and others, including: 1) the importance of habitat, particularly boreal forest ecoregions; 2) the influences of natural barriers such as major rivers and mountains particularly in eastern Russia (Safronov 2009); 3) the location of small isolated remnant and/or vulnerable populations (e.g., moose along the shared borders of Austria, Czech Republic, Germany, and the range of *A.a. cameloides* in China and northeastern Mongolia); and 4) continued expansion of moose into Central Europe. We advocate for continued examination of climate change impacts, including range expansion of potential diseases, parasites, and their host vectors (Lankester and Samuel 1998). As stated in Jensen et al. (2018), other demographic parameters that would enhance this broad-scale assessment are regional estimates of survival, pregnancy, and twining rates, accurate estimates of subsistence harvest, and age-specific mortality factors. Sharing such data should prove useful in identifying environmental factors and other influences that affect moose on a range-wide basis including climate change, fire suppression, forest management, habitat fragmentation, and the impacts of harvest strategies. By probing for patterns and using time series analyses at the landscape scale, future research may better focus on those primary factors influencing the circumpolar distribution moose.

ACKNOWLEDGMENTS

We thank the many biologists, managers, and GIS specialists that have assisted us in compiling this dataset. We also thank the reviewers for their editorial suggestions. This project was funded by Federal Aid to

Wildlife Restoration administered through North Dakota Game and Fish Department (Project W-67-R-58). Any mention of trade, product, or firm names is for descriptive purposes only, and does not imply endorsement by the U.S. Government.

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