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Review

Red Deer in Lithuania: History, Status and Management

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Abstract: The history, current population status and (un)sustainable management of red deer (*Cervus elaphus*) in Lithuania are reviewed on the basis of 57 publications and, additionally, analysis of data on numbers and hunting bag. After the extinction of the species at the beginning of the 19th century, red deer were reintroduced into the northern part of the country during World War I. Population re-establishment was further fueled after WWII by immigration from neighboring countries and local translocations. After the introduction of the Law on Hunting in 2002, which enabled hunting organizations to rent hunting grounds for longer than 10 years, local wildlife management strategies were targeted at increasing the number of animals. However, a scientifically-based target population size for *C. elaphus*, agreed by all major stakeholders, has still not been defined. In the last 20 years, population growth has been exponential, deer numbers in Lithuania being estimated as 68,816 individuals in 2021. An increase in the size of the hunting bag is necessary for the sustainable management of the species at the national scale and to avoid risks of over-population as observed elsewhere in Europe.

Keywords: *Cervus elaphus*; introduction; hunting; roadkill

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1. Introduction

The red deer (*Cervus elaphus*) in Europe is characterized by three divergent lineages (western European, eastern European and Mediterranean groups), which are related to different refugia during the last glaciation and the influence of translocations [1]. The extension of the western lineage to Eastern Europe reflects natural expansion of the species northward as well as translocations and reintroduction of red deer into areas where the species became extinct in historical times [2]. In the last two decades of the 20th century, the population size (and hunting bag) of *C. elaphus* increased across nearly all of Europe, except for the south-eastern part of the continent [3].

Overabundance is a recent trend among herbivores, having detrimental effects on the environment, ecosystem functions and biological diversity [4]. Locally, *C. elaphus* is one of these overabundant species, requiring changes to management practices and understanding of the context of the increase and trend [5]. While historically, the main factors affecting species distribution were winter temperatures and the presence of forest cover [6], the current shaping factors are land use patterns and management options [7].

Holocene changes in ungulate distribution in the north of Europe have been significant [8] and these changes have occurred in the Baltic countries also [9]. In Lithuania, *C. elaphus* was abundant until the middle of the second millennium [10], but became extinct somewhere in the beginning of the 19th century: it was still present in good numbers in 1783 [11], but was already absent in 1830 [12]. Following initial immigration from neighboring regions in Latvia between 1914–1918 [13], the population of *C. elaphus* in Lithuania has subsequently continued to increase, culminating at nearly 70,000 individuals in recent years [14]. However, our analyses (Supplementary Materials) of the population growth trends indicate virtually exponential growth so far and therefore strong population management measures are required to level further growth.

The aim of this review is to present an overview of the red deer history in Lithuania, along with the current population status, growth trends and available management options. We also seek to emphasize the necessity of sustainable species management. As there were no such data published before, we have added calculations of population growth trends (see Section 3.8 and Supplementary Materials).

2. Materials and Methods

2.1. Scope of the Literature Sources

To be analysed in this review, literature sources had to be related to both the aspects of the key species, red deer, and to the geographic scope, Lithuania. Sources covering the Baltic countries (Lithuania, Latvia and Estonia) were included in cases where Lithuania could not be singled out of the general context. For inclusion, we used a list of key terms (Table 1) related to the history, ecology and management of *C. elaphus*. We mainly used published sources, excluding student's theses, and analysed literature sources in English, Lithuanian and Russian (most of the relevant scientific literature prior to 1990 was published in Russian).

Table 1. Key terms related to red deer and used in literature search.

Key Term	Definition	Notes on Usage
Red deer	*Cervus elaphus*, member of the Cervidae family	We also used "taurusis elnias" (Lithuanian) and "blagorodnyj olenj" (Russian)
Lithuania	Territorial scope of the search	In several cases, "Baltic countries" and "north-eastern Europe" were used, as well as "Lietuva"
History	Period between last glaciation and 1830	Includes archaeological findings and published sources covering the period until species extinction
Reintroduction	Period between World War I and 1983	Reintroductions from abroad and translocations inside the country, includes "pereselenije"
Management	Includes hunting, survey and monitoring	Changes in legal background were related to changes in the hunting bag and species abundance

2.2. Search and Filtering of References

We used two online databases, the Web of Science and Google Scholar, for information retrieval. Google Scholar was inevitable, as most of the sources were not indexed in the Web of Science. Our search covered a time period from 1969 to May 2022. We used Boolean combinations: (red deer OR *Cervus elaphus*) AND Lithuania AND (history OR archaeology OR monitoring OR hunting OR management), as well as these terms in Lithuanian and Russian. Key terms are listed in Table 1.

The search yielded 104 results from Google Scholar and only 13 results from the Web of Science. A search in Google Scholar with only the Lithuanian keyword "taurusis elnias" yielded 199 results.

We excluded all master and bachelor theses (n = 65) devoted to or mentioning *C. elaphus* after finding that these sources did not contain original information on the species. After reading the remaining papers we excluded most parasitological works as they had no information on the host species, *C. elaphus*. As a result, the remaining number of publications was 57. However, many additional sources that were not found during the database searches were added as a result of examining references presented in the selected papers.

2.3. Other Data Sources

Annual numbers for the *C. elaphus* population size and the number of hunted animals (hereafter hunting bag) were obtained from the archives of the Ministry of the Environment of the Republic of Lithuania; data for recent years are available online [14]. Although these so called "official" data might have biases [15,16], there are no other data sources for the big game, and thus population management of ungulates has to be analysed with this data at the scales of the Baltic countries, Lithuania and the local level [17–22]. Data on the population size and the number of hunted animals up to the 1990s were reported in the areas of forest enterprises and later in the areas of the hunting clubs. Snow-track counts with correction by the number of visually registered animals was the main method. Number of hunted deer is the sum of used permits every hunting season, as hunters are obliged to report every kill.

Data on road-kills of *C. elaphus* are from the Lithuanian Police Traffic Supervision Service and the Nature Research Centre. In the first case, the number is a sum of reported road-kills, verified by the nearest hunting club; the second case is the number of unregistered deer road-kills found by scientists.

The study area with forest cover, main roads and the boundaries of the country's ten counties is shown in Figure 1. Data on the counties of Lithuania and forest cover dynamics are from the Official Statistics Portal [23–25]. Data on regulations concerning red deer management were collected from official sources [26–30].

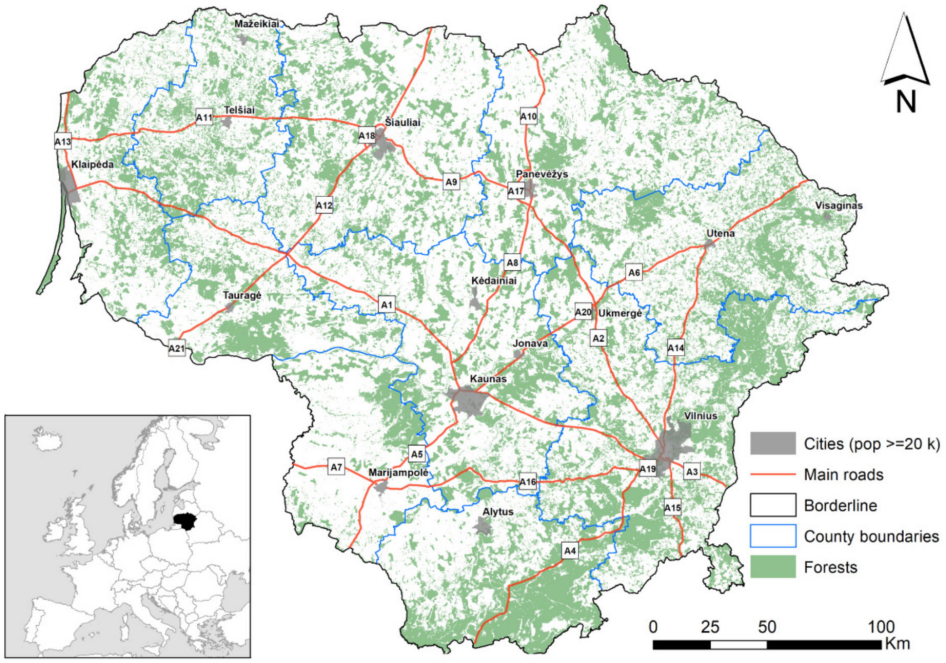

Figure 1. Lithuania, with forests and main roads in 2021. The position of the country in Europe is shown as an inset.

2.4. Data Analyses

For the management of *C. elaphus* as one of the main animals for hunting, it is important to grasp some ecological parameters such as the intrinsic growth rate and the carrying capacity. Thus, this study applies state space models for estimating these. The application of a state space model in population ecology is relatively new, but there are some existing studies including Bragina et al. [19] in which Lithuanian *C. elaphus* were also examined. Currently, the population size of *C. elaphus* appears to be increasing exponentially, thus it is useful to establish the potential carrying capacity. Therefore, both exponential and logistic growth are considered in this study. As pointed out in 2.3, the official data may be biased [15,16], because the amount of poaching is ambiguous and some roadkilled

individuals may be overlooked. As roadkill data is only available for the period since 2002, two data sets are prepared, specifically with and without the inclusion of roadkill data. Based on the above, the following four cases are considered: (Ew) exponential growth with roadkill, (Ew/o) exponential growth without roadkill, (Lw) logistic growth with roadkill data, and (Lw/o) logistic growth without roadkill data (Supplementary Materials). Regarding the proportions of *C. elaphus* in wolf diet, the existing data did not allow us to include this into the model (see Section 4).

Estimations were conducted by R and Rstan [31,32] and the code provided in Baba [33] was used with some modifications. Predictions for the trends in deer number, hunting bag and road-killed numbers were carried out using approximations of the current trends, 2003–2021, with MS Excel, partly utilizing the results of the state space model.

3. Results

3.1. Historic Presence of Red Deer in Lithuania: Holocene

Most European mammal species were affected by climate change in the Quaternary, mainly through glaciations that forced species to retract to a limited number of refugia [2]. The last glacial maximum was the main event, during which time the distribution ranges of many species were contracted to the maximum extent [34]. In terms of the red deer, the species distribution during the Atlantic Period covered most of West and Central Europe, including the Baltic Sea coasts [35]. Genetically, *C. elaphus* from Lithuanian territory was related to the West Europe haplogroup [36].

Teeth of *C. elaphus*, mostly incisors and canines, are characteristic findings in excavations of Mesolithic burials in Europe, including in the current territory of Lithuania and the neighboring countries, Latvia and Belarus [37,38]. However, antlers of red deer have not been found in burials in Lithuania, the nearest sites being in Poland. In excavations from the Late Mesolithic and Early Neolithic period, red deer bones prevail among other mammals [39,40], as the bones were used for making artifacts. In the Early Neolithic period, *C. elaphus* accounted for 35.4% of remains, while this was 31.9% in the Middle Neolithic period, 57.4% in the Late Neolithic period and 10.9% in the Early Bronze (Brass) Age [41,42]. Abundant red deer antler tools with drilled holes, these attributed to the Early and Late Mesolithic, as well as the Early Neolithic, have been found in Belarus, close to the southern part of Lithuania [43]. Similar findings from the same period are characteristic of north Lithuania [44]. Finally, the presence of *C. elaphus* in the human diet has been confirmed using stable isotope analysis [45].

As shown by Niedziałkowska et al. [6], the presence and abundance of *C. elaphus* at the beginning of Holocene was shaped by climate and habitat, namely winter temperatures and forest cover. As hunting steadily increased, this became the limiting factor that shaped the distributions of ungulates and even led to the extinction of some species [46]. Moreover, hunting shaped the landscape as, starting from medieval times, special hunting forests were established [47]. These noble hunting grounds could later evolve into protected areas, as was the case with Białowieża Primeval Forest [48]. The impact of noble hunting on game, however, was limited. In Białowieża for example, less than 20 royal hunts occurred ever [49].

In Lithuania until the Middle Bronze Age, hunting was a main economic activities [50] and *C. elaphus* was one of the main game species. During the Iron Age, hunting, as a source of meat, lost ground. In a single castle-hill (South Lithuania), the proportion of bones of game animals decreased from 27.6–35.4% in the last millennium BC to 27.5% in the first to fourth centuries, 6–7% in the fifth to ninth centuries and 3.1% in the tenth to fourteenth centuries [51]. *C. elaphus* accounted for 13–24% of all game bones in noble settlements in the thirteenth to fourteenth centuries, but only 0.03% in local farmsteads [52]. This shows that hunting had become the privilege of noblemen [50].

Game take diminished further in the sixteenth to seventeenth centuries, while *C. elaphus* was the third most abundant of the hunted species at that time, accounting for 2.9–5.6% of animals taken [53]. As proportion of *C. elaphus* taken dramatically declined in the sixteenth

to seventeenth centuries [54], this might correspond to a decreased species abundance. In the eighteenth century, *C. elaphus* was still present in Lithuania [11], but the species was already extinct at the beginning of the nineteenth century [12].

3.2. Red Deer Herd Restoration in Lithuania: 1914–1982

The comeback of red deer to Lithuania started during World War I, animals reoccupying the northern part of the country (Figure 2a). It is supposed that several individuals of *C. elaphus* escaped from enclosures of the Naryshkin noble family or were released during WWI [10]. It is also possible that there was immigration from neighboring Latvia [13]. According to [55], there were nine free living herds in the west of Latvia in 1914, with one herd located only a few kilometers from the initial location of *C. elaphus* appearance in Lithuania.

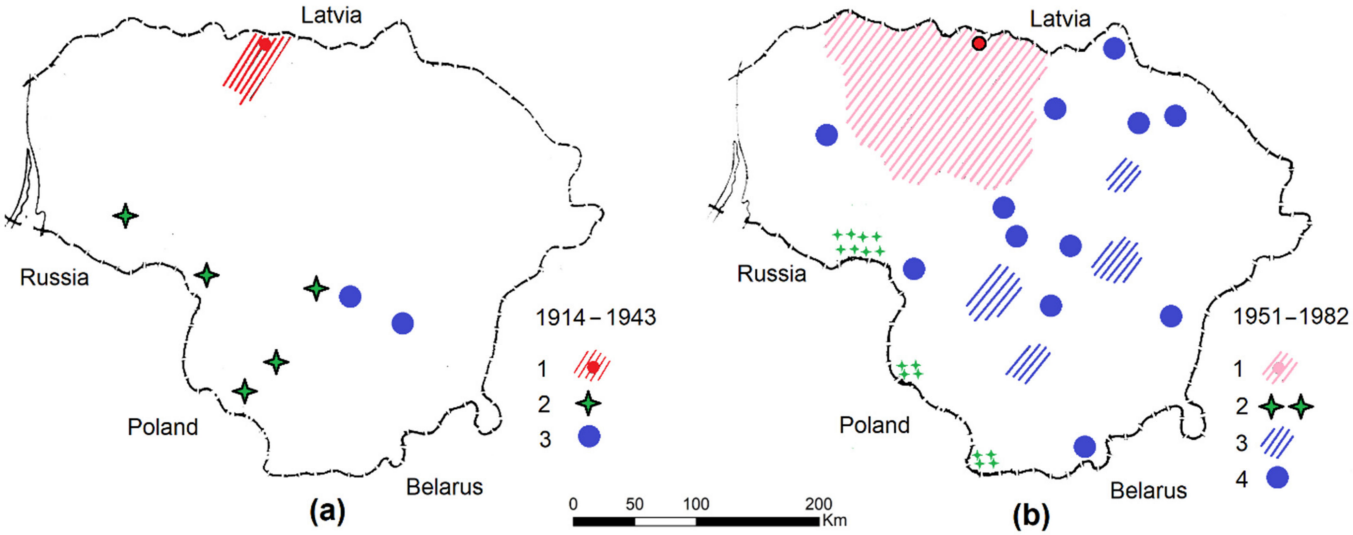

Figure 2. Reappearance of red deer in Lithuania after 1914: (**a**) first records, 1—initial location, 2—registrations of wandering individuals coming from neighboring countries, 3—first releases; (**b**) further expansion and reintroductions, 1—spread from the initial location, 2—location of herds formed by immigrations, 3—introductions, 4—records of the spreading deer groups and individuals. Redrawn from [56].

The spread of *C. elaphus* from their initial location in north Lithuania started in about 1935. Until 1938, animals were seen in the territory of one forest enterprise, but in 1940 they spread to the territory of a second forest enterprise and in the same year there were 20 *C. elaphus* registered in a third forest enterprise. By 1982, these herds had populated forests in eight districts (Figure 2b).

Immigration of *C. elaphus* into the forests of south Lithuania started later. In 1930, one individual migrated from Poland, while four individuals migrated from East Prussia in 1937 (Figure 2a). However, on the basis of immigration, a herd only formed after WW II [13]. Immigrations also continued after WWII, helping to restore herds across Lithuania and neighboring Belarus [57].

3.3. Red Deer Translocations in Lithuania: 1969–1987

First introductions and translocations were not regular: in 1935 two individuals were released into the south of Lithuania, and in 1939 two individuals were introduced from Latvia into central Lithuania (Figure 2a) [58]. To increase the spread of the restoration of the *C. elaphus* population, 51 individuals were later introduced from Voronezh Reserve (Russia): 37 individuals in 1965 and 14 individuals in 1972. This attempt was successful [10,13], though the introduced animals did not migrate [56].

Starting from 1969, translocations of local *C. elaphus* to uninhabited forests commenced [10]. At the beginning of this period, in 1969–1971, only 38 individuals were trapped in corrals, sedated and transferred [56]. This method was not effective, therefore from 1976 onwards, Komarov's bullets were used for sedation. In the 1976–1977 period, 234 individuals were translocated. In total, 801 *C. elaphus* were translocated during the period 1969–1983 (Figure 3). This helped to populate forests in 28 out of 43 administrative districts of the country [13]; 20 individuals were transferred to Estonia in 1979–1980 [56].

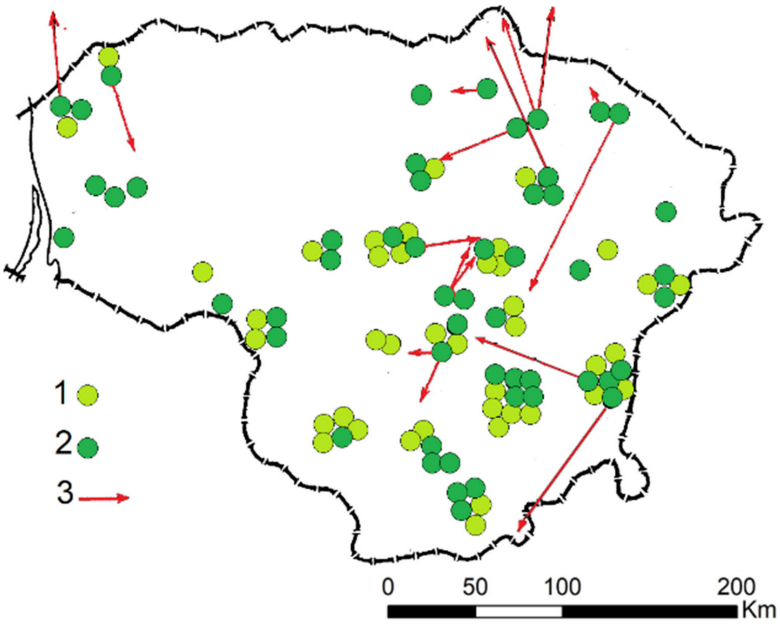

Figure 3. Red deer translocations in Lithuania, 1969–1983: 1—translocation with <10 individuals, 2—translocation with >=10 individuals, 3—direction and distance of migrations. Redrawn from [56].

In the period 1984–1987, 230 *C. elaphus* individuals were translocated within the country. The most densely populated region was the south-eastern part of the country (Figure 3). 18 individuals were transferred to Estonia in 1987, while 20 individuals were sent to Russia in 1988 [59].

As they were tagged using numbered collars, the fate of 491 transferred individuals is known: 10 of these individuals migrated to distances of 40–80 km (Figure 3) [10].

3.4. Changes in Red Deer Abundance: 1934–2021

Before WWII, the growth of the *C. elaphus* population in Lithuania was mainly supported by immigration and therefore was quite slow (Table 2). From 18 individuals registered in 1934, the number of *C. elaphus* grew to 99 in 1937 [60], 190 in 1939 and 239 individuals in 1943 [10]. After WWII, due to perturbations and poaching, numbers declined by two-thirds, and it then took nearly another 10 years to reach 300 individuals (Table 2). The slow increase in the abundance continued until 1967, the period being characterized by a see-sawing in the annual growth percentage (Figure 4).

Table 2. Red deer numbers (N), hunting bag (H) and road-kills (R) in Lithuania, 1934–2021. There are no data for the years not shown.

Year	N	H	Year	N	H	Year	N	H	Year	N	H	R
1934	18	0	1962	570	0	1983	9700	2784	2002	11,098	1288	5
1935	40	0	1963	570	0	1984	10,000	3351	2003	10,584	833	7
1936	92	0	1964	670	0	1985	10,900	2841	2004	11,199	0	7
1937	99	0	1965	830	0	1986	11,900	3895	2005	12,417	574	4
1938	173	0	1966	900	0	1987	13,200	2619	2006	14,400	766	7
1939	190	4	1967	900	0	1988	12,500	3994	2007	15,912	869	11
1943	239	0	1968	1050	0	1989	13,800	3793	2008	16,995	1027	6
1948	101	0	1969	1300	0	1990	13,400	4736	2009	18,978	1158	13
1949	120	0	1970	1800	0	1991	14,500	3989	2010	21,303	1380	6
1950	122	0	1971	1850	20	1992	14,890	4322	2011	23,495	1496	16
1951	130	0	1972	2500	35	1993	13,391	3724	2012	25,672	1602	11
1952	170	0	1973	3000	60	1994	13,822	4597	2013	28,137	2075	27
1953	205	0	1974	3220	152	1995	13,800	4006	2014	30,056	2467	28
1954	254	0	1975	3600	405	1996	13,900	2135	2015	33,318	3204	34
1955	277	0	1976	4000	366	1997	15,000	2176	2016	36,147	3857	44
1956	300	0	1977	5000	278	1998	16,071	1768	2017	41,266	5266	34
1957	298	0	1978	5300	1059	1999	15,429	2099	2018	47,380	6405	78
1958	323	0	1979	6000	1144	2000	15,181	2028	2019	55,254	7876	120
1959	356	0	1980	7300	1326	2001	12,663	1306	2020	61,314	8968	76
1960	380	0	1981	8000	1971				2021	68,816	9048	100
1961	480	0	1982	9100	2639							

Data sources: numbers and hunting bag–Ministry of Environment of Republic of Lithuania and Laboratory of Mammalian Ecology of Nature Research Centre; road-kills–Lithuanian Police Traffic Supervision Service and Nature Research Centre.

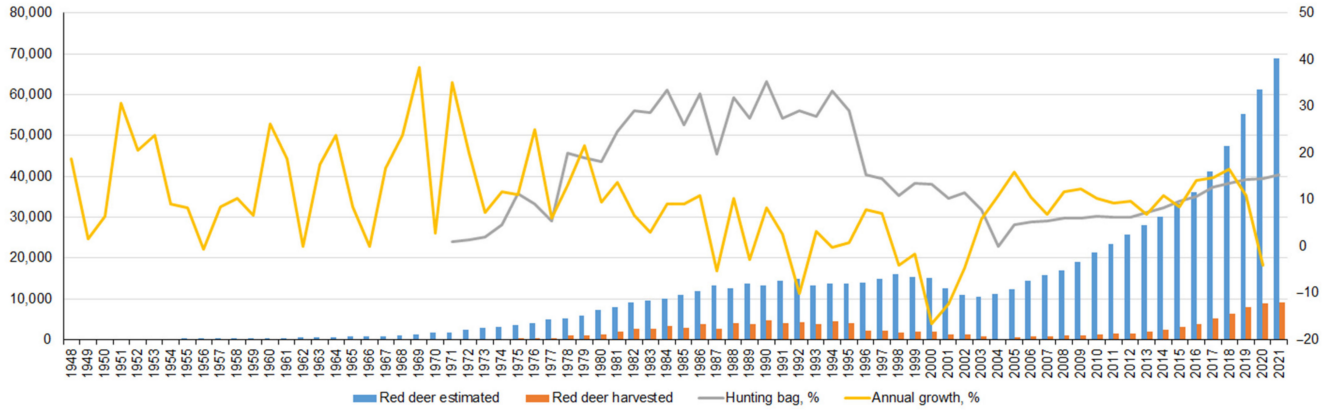

Figure 4. Trends of red deer numbers, hunting bag, proportion of hunted animals and annual population growth in Lithuania, 1948–2021.

After 1968, due to immigration and translocations, the number of the *C. elaphus* soon exceeded 1000 individuals, thereafter reaching 2000 between 1971 and 1972, 3000 in 1973 and 4000 individuals in 1976 (Table 2). From 1971, the hunting of red deer started.

The intensity of hunting (as % from the surveyed winter deer number) was not stable: it was over 20% (with a maximum over 30%) in the period 1981–1995, while only 10–20% in 1978–1980, 1996–2002 and 2016–2021 and less than 10% in 2003–2015 (Figure 4). After intensive exploitation, growth of deer numbers was thereafter retarded: in the years 1998–2003, the *C. elaphus* population decreased. As a management measure, the quota for *C. elaphus* was minimized for the period 2003–2007, being <1000 deer. In 2004, the hunting quota was zero (Table 2). As lowering the quota did not halt the population decrease immediately, it can be concluded that poaching was having a negative impact [61].

A somewhat similar situation in terms of *C. elaphus* re-establishment was found in neighboring Latvia, where active reintroduction into unoccupied areas in the north and east

of the country was conducted in 1963–1988, translocating 386 individuals [62]. However, despite population growth in Latvia and Lithuania, both countries were reported as having problems with overharvesting of *C. elaphus* [19].

The densities of *C. elaphus* have increased dramatically in recent decades (Figure 5), with the maximum average density being 62.6 and 66.7 individuals per 1000 ha of forest in the two counties in 2021. In general, the highest densities are characteristic to the counties that saw immigration of the deer after WWII (two northern counties in 2005, Figure 5b; the same northern counties and one southwestern county in 2015, Figure 5c; the same plus neighboring counties in 2021, Figure 5d). The densities of *C. elaphus* do not correlate with forest percentage in the counties (Pearson's r = −0.55 in 2021, r = −0.50 in 2015 and r = −0.47 in 2005, all significant at $p < 0.05$). These correlations prove that forest area is not the main factor controlling the maintenance of herds of *C. elaphus*.

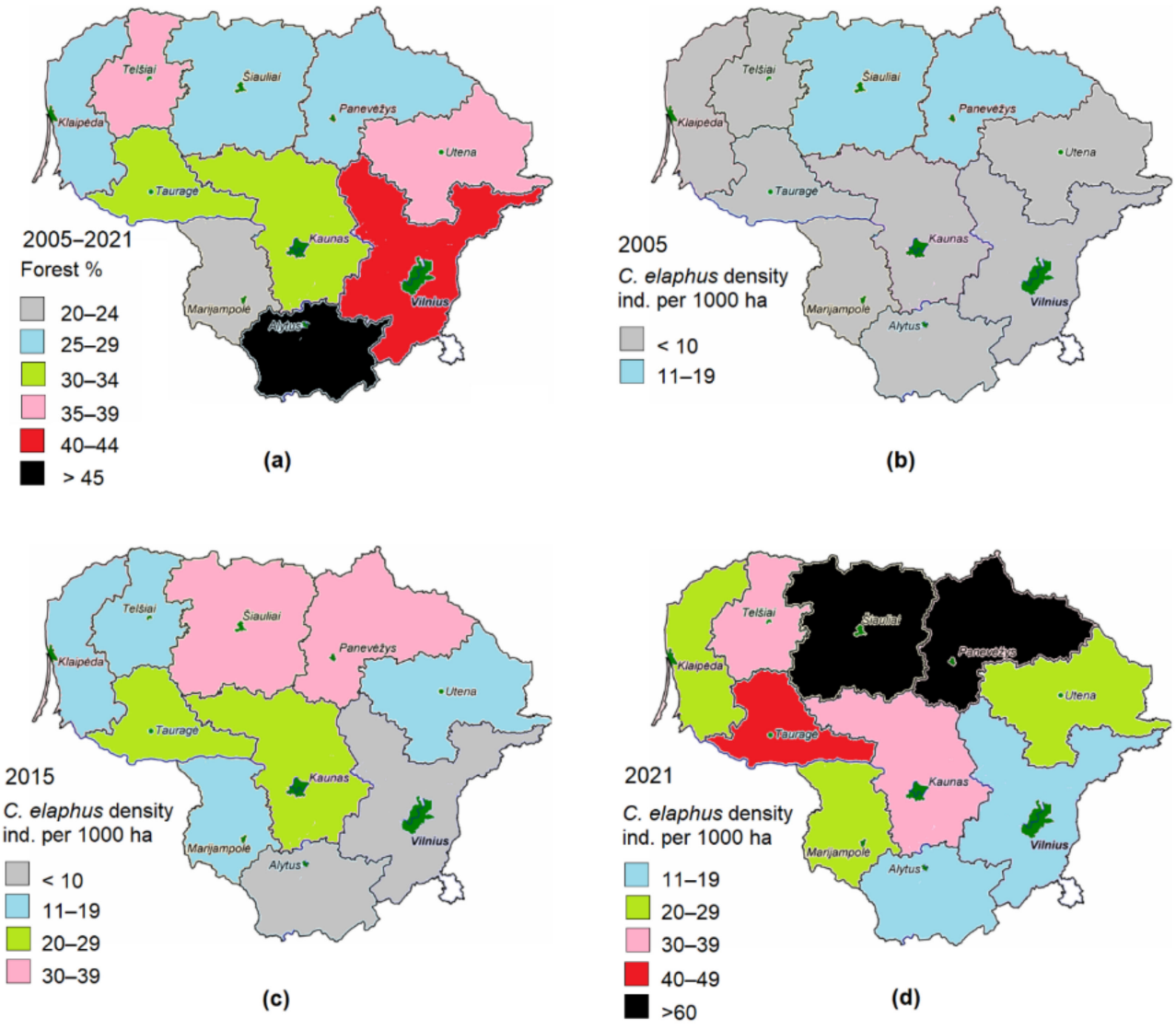

Figure 5. Forest percentage and red deer densities in 10 counties of Lithuania: (**a**) forest percentage, (**b**–**d**) red deer densities in 2005, 2015 and 2021. Locations of county centres indicated in dark green.

3.5. Red Deer Ecology: Adaptation to Anthropogenic Habitat

Being widely distributed across Europe, *C. elaphus* is an ecologically flexible species, inhabiting a wide array of habitats [63] and foraging on various plant materials, such as trees, shrubs, grasses, sedges and herbs [64,65]. These animals may live and prosper in re-cultivated habitats [66]. As well as hunting, winter foods [67] as well as wildlife and

forest management measures [68] are main factors that regulate red deer numbers and habitat use.

In the period covered by this review, Lithuania has seen significant changes in the main habitats available. In the Medieval Period, the main habitat of the country was forest, but forest areas were considerably less by the time that *C. elaphus* re-established in 1918, the forest areas reaching a minimum of 19.7% in 1948 [69]. Due to intensive afforestation of agricultural or abandoned lands, forest cover has since increased, reaching 30.1% in 1993 and 33.2% in 2018 [70].

To sum up, the re-establishment of *C. elaphus* in Lithuania has coincided with significant landscape changes. Before 1940, agricultural lands were fragmented due to private ownership and small-scale production. During the Soviet period, large collective farms emerged after land nationalization [71]. From 1945 to 1990, natural patchiness was lost and land reclamation covered ca. 80% of swamps. After 1990, small-scale agriculture returned along with a drop in the levels of chemical agents and heavy machinery used. The area of abandoned land in Lithuania was 18% in 1998 [72].

There are no published studies in Lithuania on habitat use by *C. elaphus* prior to 1970. Forests were presumed as the main and nearly only habitat of the species [73–75]. Later, however, the importance of surrounding agricultural lands was recognized [13,76]. At very high densities, reaching a maximum of 240 *C. elaphus* per 1000 ha of forest habitat, animals used agricultural lands for feeding all year round [76]. As such, animals were able to source supplementary provisions from the fields, this being the main factor that allowed deer numbers to explode [77,78]. In addition, the importance of the vegetation remnants after clearcutting (branches and bark) as a food source for cervids was acknowledged [79,80]. The influence of other factors, such as forest stand composition [81,82] and the presence of dwarf shrubs [83] was also said to have an influence on the spatial distribution of *C. elaphus*.

Later publications on *C. elaphus* ecology in Lithuania put an accent on areas of forest–agriculture transition and forest edges [84], as well as total forest area, density of roads and urbanization [85]. All of these highlight the importance of human-made landscape conversion.

3.6. Red Deer Damage, Allowable Densities and Population Monitoring

After numbers of *C. elaphus* increased to over 5000 individuals, discussions of damage to forest stands in winter started, initiated by scientists of the Forest Research Institute. As a result, publications on the regulation of *C. elaphus* abundance [86] as well as that of other cervids in Lithuania appeared [87].

Data on cervid damage to forests are available for the period 1967–2021 [88]; however, evaluation methods and presentation formats differ (see Section 4). In 1967–1997 forest area damaged by *C. elaphus* correlated with deer abundance ($r = 0.86$, $p < 0.001$) and increased from 769 ha [89] to 7135 ha [90]. Maximum damages done by all cervids (red deer, moose and roe deer), exceeding 20,000 ha of forest, were recorded in 1990–1994 [91]. In 1998–2021, forest areas damaged by all cervids decreased as a consequence of prevention measures, such as repellents and fencing ($r = -0.92$, $p < 0.001$). In 2021, forest area damaged by cervids was 2141.9 ha [92]. However, structured data on the damage of cervids agricultural lands are not available.

To prevent damage by deer browsing, allowable densities according to the type of forests were set [93], these further being developed into fundamentals of game management [94]. In Lithuania, these densities were and still are named as "norms". Economically allowable densities presume an uneven distribution of individuals and that the consumption of natural foods does not cause damage to forest and agriculture, and therefore are designated as "permissible". Ecological densities presume that the requirements of natural foods are equal to their resources, the negative influence of cervids on forest and agriculture becoming significant. At upper ecological densities, animals are evenly distributed across all available territory and damage is considered unacceptable. These densities were labelled as maximum allowable densities [26]. In the case where several species of cervids share

the same territory, densities should be recalculated, depending on the moose and roe deer numbers (Table 3).

Table 3. Densities of cervid species (individuals per 1000 ha of the habitat) in Lithuanian forests: P—permissible, or economically allowable, E—ecological [93], M—maximum allowable [26].

Forest Type	Red Deer *			Moose			Roe Deer		
	P	E	M	P	E	M	P	E	M
Deciduous, deciduous with fir	10–20	21–25	15	4–5	6–7	4	40–60	50–80	55
Mixed fir and deciduous	10–15	16–20	12	3–4	5–6	3	20–40	30–50	45
Mixed pine and fir	10–15	16–20	12	2–3	3–4	2	20–40	30–50	35
Pure pine stands	4–8	5–10	6	1–2	2–3	1	10–20	10–20	15

* if *C. elaphus* cohabit with other cervids, allowable densities should be recalculated, presuming one moose equals three red deer, and one red deer equals four roe deer. Densities in forests <300 ha with a distance over 1 km from bigger forest areas are not limited.

For several decades, the densities of *C. elaphus* and other cervids in Lithuania were surveyed using pellet counts, a method based on the works of Bennet and McCain [95,96]. This method was developed further to allow not only the assessing of their number and browsing pressure, but also the structure of their populations based on pellet size and form [97]. The method was used for state-wide cervid monitoring [98–101] and research [22,102] until very recently. From 2018 onward, cervid monitoring has been done using winter track counts as an index of relative abundances [103].

3.7. Legal and Administrative Background of Red Deer Population Management in Lithuania

The main, indeed the only, management tool in the current day for deer population control is hunting. It is done with the purpose to regulate deer numbers, to reduce damage done to forest stands and surrounding agricultural areas and to maintain population integrity. While hunting for damage control is not very common in Lithuania, recreational hunting is usual [18]. There are also commercial hunting grounds, where red deer densities are kept at a maximum, exceeding maximum allowable numbers and harvested more intensively [22].

Hunting intensity is regulated through quotas, issued annually in the Republic of Lithuania and approved by the Minister of the Environment [28]. The quota for *C. elaphus* in Lithuania is calculated on the basis of data presented by municipal commissions for limits on game animals. Limits are set bottom up, based on proposals by each hunting ground owner. In the proposal, the number of *C. elaphus* present, the number to be hunted in the next season, the bag size of the previous season and amount of damage done by cervids are presented. The limit should be set by 15 April, but can be reconsidered during the hunting season. Any limit increase over 50%, however, has to be approved by the regional Department of Environmental Protection. An additional quota may be issued if there is significant damage done, or if deer density is over two times the maximum allowable [29].

Looking back, there are several periods with important legal and administrative changes related to *C. elaphus* population management in Lithuania [10,18]. Arranged as a timescale, they are presented in Table 4.

Table 4. Legal and administrative changes related to moose population management.

Period	Characteristic	Impact
1950–1970	Hunting ban	Fifteen-fold increase in the population, from 122 to 1800 individuals (see Table 2).
1971–1988	Soviet period	*C. elaphus* were hunted to deliver meat to state-owned meat factories and to export for hard currency [104], obtaining 2–3 million rubles annually [105]. Hunters were not interested in increasing the number of deer [106].
1978–1995	Period of the highest hunting pressure	The hunting bag set at 18–35% of the winter population (Table 2). A negative opinion prevailed regarding deer as a source of forest damage [75,86,87]. This period finally ended with the transfer of hunting management to the Ministry of Forestry in 1989, though overhunting continued until 1995.
After 1990	Independence of Lithuania	Period of reorganization with a simplified procedure introduced for the possessing of guns by farmers for self-defense. Lack of hunting control resulted in a rise in poaching levels [100]. In 1995, regulation and control of hunting were transferred to the Ministry of Environmental Protection, resulting in a drop in the hunting bag to 10–15% of the winter deer numbers (Table 2). Several documents related to *C. elaphus* population management were adopted, namely the Regulation for Hunting in the Republic of Lithuania and the Rules of Hunting in the Republic of Lithuania [27–30].
1995	Hunt regulations	Regulation for Hunting in the Republic of Lithuania and the Rules of Hunting in the Republic of Lithuania (consolidated edition at [30]).
2002	Law on Hunting	Concepts of hunting, hunting plot units (order of designation and size) and selection established [21]. Hunter organizations were enabled to rent hunting grounds for terms no shorter than 10 years and, as a consequence, they obtained the possibility of adopting long-term wildlife management strategies. This was followed by a drop in the hunting bag to below 10% in 2003–2015, increasing the abundance of *C. elaphus*. Consolidated edition of the Law on Hunting can be found in [103].
2021	Selective deer hunting ceased	No regulation regarding selective deer hunting [30], so apart from the quota the only other regulation in terms of hunting is the length of the hunting season. Since 2020, deer stags can be hunted from 15 August to 31 January, does and calves from 1 October to 31 January [29].

3.8. Results of Data Analyses and Implications for Red Deer Population Management in Lithuania

The above results and calculations (Supplementary Materials) might indicate the following. First, currently, the population size of Lithuanian *C. elaphus* is increasing virtually exponentially, and additional data is required to estimate the carrying capacity. Second, when applying logistic growth, there are no clear differences in the estimated values of the intrinsic growth rate when including and excluding roadkill data (Lw and Lw/o). On the other hand, the results may be biased in the exponential growth case when roadkill data is not available. It is recommended to apply a logistic growth equation in real-life applications even if the population exhibits exponential growth when estimating population parameters such as r and K using the state-space model.

We may conclude that *C. elaphus* is a widespread and abundant game species in Lithuania, with a large potential to see further population growth under the current management format. The possibility for owners of hunting plot units to plan and implement deer management through the size of the annual hunting bag had a much greater impact than other regulations. However, Lithuania still has no long-term strategy of *C. elaphus* population management, therefore population numbers have been growing at a nearly exponential rate since 2003. It is not clear what the influence of revoking the requirement on selection in stag hunting will be [107]. Nonetheless, increasing the hunting bag is necessary for sustainable species management at the country scale. Otherwise, predictions using current population growth trends show unacceptable levels of *C. elaphus* abundance and increase in roadkill numbers (Figure 6).

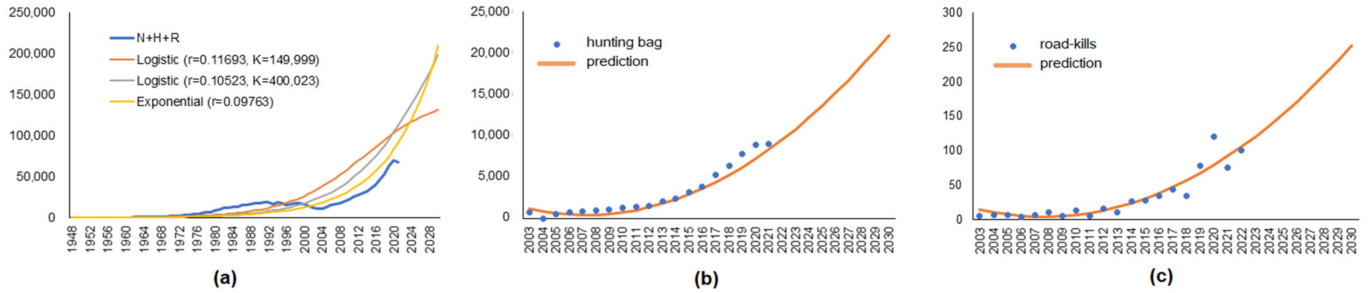

Figure 6. Prediction of the growth of *C. elaphus* numbers (**a**), hunting bag (**b**) and numbers road-killed (**c**) in Lithuania, 2030.

The acceptability of deer abundances, however, differs between stakeholders: foresters followed by farmers, are in favor of the most limited numbers and densities of *C. elaphus*, as both groups incur significant level of damage. In contrast, hunters favor increasing numbers of *C. elaphus* and thus limit their bag (and do not request increased quotas). Views of those in two different groups simultaneously (e.g., forester- or farmer-hunter) might be uncertain. As yet there is no scientific plan for management of the species in the country and our position for sustaining current deer numbers was based on the growth prospect and subsequent increase of related road-kills.

4. Discussion

Red deer, as well as many other ungulate species, have increased their numbers in many European countries over the last decades, becoming locally overabundant [4]. Growth in *C. elaphus* numbers was characteristic of nearly all former-Soviet European countries after the collapse of the socialist regime, perhaps excluding Ukraine [19]. Changes in land use (including abandonment of agricultural lands, afforestation and urbanization) and changes in legislation were two very important factors, confirmed also in our review conducted for Lithuania.

Spread of *C. elaphus* across the country from the places of introduction or immigration took decades, but is now finished. The increasing number of deer has resulted in damage to forests and agriculture, as well as to increased numbers of collisions with transport. These will not be successfully solved with current management approaches [4,5,17,18]. Benefits associated with hunting and tourism do not counterweight these issues [4]. Therefore, a scientifically-based management plan is needed for *C. elaphus*, including effective monitoring, planned hunting limits and human dimension studies to balance species acceptability, by stakeholder groups [16–18]. We found this to be urgent for Lithuania, though also relevant to other Baltic countries experiencing similar management problems [18]. We understand sustainability of *C. elaphus* management as conforming to several conditions: (a) sustaining long-term stability of deer numbers without the wild fluctuations shown in Figure 4, (b) defining a scientifically-based target *C. elaphus* population size, agreed by all major stakeholders, and (c) stabilizing the hunting bag ratio to deer number over long periods. The current *C. elaphus* management approach is not sustainable, as it has allowed the exponential growth of population numbers in the last decade. The current increase in hunting limits shows a lack of consistency at an administrative level. For the 2022–2023 hunting season, the proportion of stags in the limits of the administrative districts varies from 20.6 to 40.8% [108], thus showing limited possibilities to control population growth and the different positions of the hunters in maintaining population structure. The same unsustainable management was reported for moose in the country [21].

Changes in methods for surveying deer numbers and their damage hinder effective comparisons and evaluation of trends. For example, the evaluation and reporting of damage by *C. elaphus* on forest stands and saplings across the 1968–2021 period differed. Until 1990, the area of damaged forest stands and saplings was evaluated in respect to each individual cervid species, i.e., moose, red deer and roe deer damage was differentiated, as

shown in [88,89]. At the country scale, the damaged forest area was calculated as a sum of damage, annually reported by forest enterprises. These reports were validated on site by representatives of the Group of Forest Pathologists under the Ministry of Forestry. Since 1990, however, cervid damage has been differentiated as shoot browsing, debarking and crown breaking, with the first two damage types presented for the three cervid species combined, while the last for moose only [88,91,92]. Therefore, evaluation of *C. elaphus* damage and calculation of long term trends is not possible. Since 2015, the evaluation of dead and seriously damaged trees has been conducted in sample plots (radius 4 m) established diagonally across damaged areas [109].

Knowledge of unbiased deer numbers is essential for effective management of their populations [7,16,18]. Lithuania, however, currently uses only a relative index based on the snow track counts [103]. While former investigations confirmed the importance of agricultural areas all-year-long, the main factor that allowed deer numbers to explode [76–78], the current ecology of the species, including habitat selection and damage to agriculture, is not the object of scientific research.

The number of wolves in Lithuania was about 1000 in 2018 [110]; however, published data on wolf diet allow us to conclude that the impact of wolf on *C. elaphus* numbers is not significant. Red deer was not on the list of prey items recorded in Estonia or Latvia [111–113], while the proportion of all cervids in their diet in Latvia and Lithuania is reported at about 50% [114,115]. In Germany, the diet of the wolf population in the period of increase after initial immigration included 21% *C. elaphus* and 55% roe deer, *Capreolus capreolus* [116]. From [117], we may presume that wolf predation on *C. elaphus* increases in natural forests, which is not the case in Lithuania.

Finally, for the successful management of *C. elaphus*, evaluation of the extent of stakeholder-deer conflicts is necessary as well as balancing opinions regarding species acceptability.

5. Conclusions

The exponential growth of *C. elaphus* numbers in Lithuania since 2003 is not balanced by a respective increase in the hunting bag and, therefore, management of the species is not sustainable. If the trend continues in this way, the existing overabundance will lead to the carrying capacity of the habitat being reached in the next decade. A long-term strategy is needed at various administrative levels to ensure that individual hunting plot managers give due consideration to public needs regarding safety and ecosystem services.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/su142114091/s1, Figure S1: Estimates of the intrinsic growth rate with a 95% confidence interval; Table S1: Estimation results of the state-space model.

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