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Dynamics of distribution of introduced mammals in Ukraine and factors influencing them

I. Zagorodniuk*, D. Lazariev**

** National Museum of Natural History, NAS of Ukraine, Kyiv, Ukraine*
*** I. I. Schmalhausen Institute of Zoology, NAS of Ukraine, Kyiv, Ukraine*

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National Museum of Natural History, NAS of Ukraine, Bohdan Khmelnytsky st., 15, Kyiv, 01054, Ukraine. Tel.: +38-066-210-57-23. E-mail: zoozag@ukr.net

I. I. Schmalhausen Institute of Zoology, NAS of Ukraine, Bohdan Khmelnytsky st., 15, Kyiv, 01054, Ukraine. Tel.: +38-044-235-10-70. E-mail: lazarevden@ukr.net

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This article considers changes in the composition of the fauna and in the abundance of alien mammals from the group of introduced species over the past two decades, which in Ukraine are marked by two powerful processes. These are the distinct processes of climate warming and shortening of winters, on the one hand, and the large-scale war waged by Russia against Ukraine on the territory of Ukraine, on the other. Such changes in the natural environment lead to significant shifts in the boundaries of natural zones and, accordingly, the living conditions of all species, not only local biota but also aliens. Among the latter, a special group is made up of introduced species, as those that appeared not as a result of natural dispersal in the context of global climate change, but due to various types of introductions. Among them are three species from the superorder Rodentia (*Oryctolagus cuniculus*, *Ondatra zibethicus*, *Myocastor coypus*), three species from the superorder Carnivora (*Nyctereutes procyonoides*, *Neogale vison*, *Procyon lotor*), five species from the superorder Ungulata (*Cervus nippon*, *Dama dama*, *Ovis gmelini*, *Equus hemionus*, *Equus ferus*). The following five factors contributed to the success of the introductions: 1) captivity with the possibility to escape, 2) destruction of various kinds of nurseries (during the war), 3) reduction of the abundance of native species, 4) increase in the share of degraded habitats, 5) reduction of all forms of nature use and population regulation. The factors of successful introductions are analysed in terms of habitat types and the structure of guilds in which the introductions are integrated. It is shown that introductions of species confined to eutrophic habitats and species occupying 'windows' or marginal places in the guild structure are successful. Most of the introductions carried out in Ukraine have resulted in the formation of natural populations of alien species, mainly semi-aquatic mammals: rodents (*O. zibethicus*, partially *M. coypus*) and carnivores (*N. vison*, *N. procyonoides*). Terrestrial species did not show significant expansion and naturalisation, with the exception of the sika deer. The increase in the number of some alien species (*O. zibethicus*, *C. nippon*, *N. vison*) occurred simultaneously with a decrease in the number of their competitors from the native fauna (*Arvicola amphibius*, *Cervus elaphus*, *Mustela lutreola*). The most problematic was the entry of *N. vison* into the mustelid guild. The appearance of alien species has led to the extinction of a significant part of ecologically similar native species, and the total number of these two groups of animals has become almost equal. Hunting of animals as a means of regulating their populations has proved to be ineffective, as the volume of hunting is 1–2 orders of magnitude lower than the annual population growth of these species, which indicates that alien species are not vulnerable to hunters.

Keywords: introductions; alien species; population; guild; habitats; climate; warfare ecology.

Introduction

The last two to three decades in Ukraine have been marked by significant changes in nature associated with climate warming, rising temperatures, shorter snow and frost periods, and, in the south, the disappearance of winters as a phenomenon (Boychenko et al., 2016; Vozhegova et al., 2021; Pichura et al., 2022). In addition, over the past 10 years, these processes have been amplified by the impacts of the war in eastern and southern Ukraine, which has led to the devastation of natural complexes, including large-scale disturbances of soil and vegetation, fires, and destruction of biotic communities (Zagorodniuk & Vyshnevskyi, 2022). At the same time, this is accompanied by the dominance of a number of unnatural impacts, including the saturation of water and soil with explosive chemicals, the formation of a belligerative landscape (Denysyk et al., 2023), the release of high energy, etc. All of this affects changes in the composition of the fauna, and one of the most prominent processes is the promotion of alien species by military activity (Zagorodniuk, 2024).

Alien mammal species have become an integral and notable component of the fauna of even remote mountainous regions, such as the Skole Beskids (Stetsula, 2019), as well as coastal regions, including biosphere reserves, such as the Black Sea Biosphere Reserve (Korolesova et al, 2019), not to mention the economically developed and urbanised regions, which are overrun with alien species with a fauna rotation index of over 15–20% (Zagorodniuk, 2010). Among such alien species, a significant proportion are introduced species, i.e. species introduced into the local biota that are intentionally introduced or have escaped from culture, and in some cases have both the status of introductions (in adjacent territories) and invaders (from adjacent territories) that have come to new places on their own, as a result of reproduction and dispersal without human intervention.

The obvious consequences of climate change have been changes in the ranges of a number of species that were limited in distribution in Ukraine or known only outside the country. Such changes resulted in the emergence and widespread expansion of new species, the most prominent and well-known examples of which in the fauna are Kuhl's pipistrelle and the golden jackal (Zagorodniuk, 2006; Rozhenko, 2017), and changes in the ranges of a number of native species (Zagorodniuk, 2022). Climate change, given the temperate climate and the corresponding natural zonation, leads to significant shifts in the boundaries of natural zones and, accordingly, to changes in the living conditions of all species, not only local biota but also invasive species. And such changes, which are rather unfavourable for the natives, may turn out to be favourable for the introduced species, which will lead to their population growth.

The topic of invasive species is extremely broad, in particular due to the diversity of their origin and current status (Zagorodniuk, 2006; Kucher, 2014). Within the vertebrate fauna of Ukraine alone, we consider 54 species, which, by their origin and current status, represent 9 nominations – three groups with three subgroups within each of them (Zagorodniuk, 2023b). Of these, a special group is made up of introduced species. Unlike natural invaders, which disperse along natural gradients and due to their historical changes, the peculiarity of this group is local introductions with the formation of introduction centres and their subsequent acclimatisation, and usually secondary natural (rarely additionally artificial) dispersal within the acclimatisation zone. In fact, this review is dedicated to them.

Importantly, the topic of introductions as the most prominent part of regional faunas was shaped by hunting ground improvement programmes (Fortunatov, 1933; Sakhno & Simonov, 1956; Sakhno, 2015), which were later replaced by reintroduction and rewilding programmes (Trouwborst & Svenning, 2022; Hart et al., 2023; Sheihas, 2023). Despite these still common practices, alarm bells are being raised around the world about the extremely high proportions of alien species, including artificially introduced ones, and their negative impacts on native biota (Parker et al., 1999; Sanders et al., 2003; Blackburn et al., 2019). In Europe, the issue of compiling lists of alien species and estimates of their damage to biodiversity and the economy has long been raised (Carboneras et al., 2018; Tedeschi et al., 2022).

The purpose of this paper is to summarise the entire body of available data on the part of the Ukrainian mammal fauna that is composed of introduced and partially reintroduced species, to analyse long-term changes in their population dynamics and distribution, to assess their current geographical ranges within Ukraine, and, based on these data, to analyse the impacts of three groups of factors on populations of introduced species: climate change, anthropogenic environmental changes, including formation of belligerative landscapes in the context of the ongoing war on a large part of Ukraine.

Overview of information sources

This work is analytical and combines data from various sources: from the results of open source information searches (OSINT searches) to the analysis of official hunting statistics and literature data, combined with data from our own observations and research of museum collections, as well as interviews with colleagues. This section discusses the most important features of searching and accumulating data, analysing statistics, and determining the reliability of data received from respondents.

The authors use six types of data sources that are important for a monitoring system. Their brief description is as follows: 1) direct data from field surveys – a group of sources that makes up a small share of the total dataset, but is important for confirming and verifying data on the existence of alien species in certain regions; 2) OSINT-search – a source that provides the largest amount of actual data on alien species. Such data were obtained through surveys and media analyses. Particular attention was paid to confirming the data obtained, which is described further in the methodology; 3) analysis of public databases and profile pages in social networks (a significant number of finds were based on the messages of respondents in the Facebook group 'Animal World of Ukraine'), databases of animal finds (INaturalist, Biodiversity of Ukraine Data Centre, UkrBIN). 4) literature analysis – a review of relevant zoological literature to obtain data for analysing the dynamics of the spread of alien species, including changes in the fauna as a result of military operations and climate change; 5) state statistical reporting – review and analysis of long-term population records in the form of '2tp-hunting' (including hunting bag statistics) obtained from the State Statistics Service of Ukraine, which allowed us to analyse the dynamics of the numbers, bagging and distribution of alien species in Ukraine and in certain regions. This important part of the data is described separately below; 6) communication and consultations with colleagues to collect data on changes in the fauna and ecology of alien and native species, primarily game scientists, hunters, foresters, other nature users, colleagues from protected areas, and various amateurs whose data could be verified.

To analyse and visualise the results, we used two main options for graphical representation of the data: plotting the series of long-term changes in the number of animals (the scale of harvesting was also analysed separately) and cartographic analysis of the spatial distribution of numbers (or separate finds). Graphical materials are based on data from open sources and literature, but the graphs and maps themselves are the original results of the analysis. An overview of the species and examples of the use of such data is provided below.

To estimate the total number of species, its changes over time, and the spatial distribution of such survey results (by administrative regions of Ukraine), we used data from the state statistical reporting form '2tp-hunting' (full name: 'Form No. 2-tp (hunting): Report on hunting management for [year]', State Statistics Committee of Ukraine, 2010. www.ukrstat.gov.ua). These data were compiled by the authors using the archive of the State Statistics Service of Ukraine for 1983–2021. Below are details on the use of state statistics data for specific groups of alien mammal species.

Rodents. Data on the abundance of coypu in official statistics are provided only in some years. For example, in 2002, the number of coypu in Donetsk Oblast was reported as 35 individuals, and in Zhytomyr Oblast in 2009 31 individuals. In subsequent years, both for these and other regions of Ukraine, data on the coypu population are not available. Presumably, these facts (counted coypu) are due to the survey of animals released by humans rather than wild ones or those that escaped from breeding sites but did not form a stable population that would exist in subsequent years.

Carnivores. The numbers of *Neogale vison* as a separate biological species have been recorded only since 2011 under the name 'American mink', thus correcting the previous unjustified lumping of two mink species, 'American' and 'European' mink, into one category called 'free mink', which was criticised (Zagorodniuk & Dykyy, 2012). Nevertheless, the name 'free mink' remains as a separate survey category (except for American mink), which 'theoretically' takes into account the abundance of *Mustela lutreola*. The commonly used name 'European mink' appeared in the statistics only in 2018, thereby replacing the name 'free mink' and finally separating the native species (*Mustela lutreola*) from the alien one (*Neogale vison*). Since 2011, statistics have included data on the jackal (*Canis aureus*), despite the fact that the species had started to expand 10 years earlier (Zagorodniuk, 2006). Raccoon dogs (*Nyctereutes procyonoides*) have been recorded in the 2tp statistics since 1992.

Ungulates. Red deer (*Cervus elaphus*) and sika deer (*Cervus nippon*) were split into separate survey categories in the inventory only in 1992; before 1992, there was a common category of 'deer' (actually the genus *Cervus*), without any division into alien and native species.

For all species, detailed information is provided on the history of introductions, long-term changes in abundance during the period of statistics for each species (from the 1980s and 1990s to 2021), an analysis of range expansion and the current state of populations and geographic distribution. In the descriptions of each species, as far as possible, all key references to the study of introductions are given, plus the two figures indicated above: a graph of the long-term population dynamics and a map of the distribution of the species on the territory of Ukraine. In the descriptions of population dynamics, in cases where data on earlier monitoring periods were available, in particular for muskrat and 'free-ranging mink', the data cover the period from 1983.

For species that have not undergone naturalisation and that have not formed stable natural populations (in particular, for which there are no statistical reporting data of 2tp-hunting), as well as for some others, for which the available literature and statistical data needed to be supplemented, data on the actual findings of animals is given in the form of cadastres, with attention to finds in the last 20 years.

Such additions were necessary in the case of *Ondatra zibethicus*, due to the incompleteness of the statistical data, in particular due to the apparently incorrect information about the absence of the species in Zaporizhzhia Oblast and in the Crimea, which is given in 2tp. For *Myocastor coypus* and *Procyon lotor*, it is important to present a list of actual findings, since literature and statistical data about their distribution areas and abundance in Ukraine have not been available until now. For such species as *Nyctereutes procyonoides* and *Neogale vison*, detailed data on their records on the borders of their ranges are provided for the analysis of their possible expansion to new territories. Finally, we also provide data on places of distribution of *Equus hemionus* and *Dama dama*, the finds of which are locally restricted. Cadastres are not presented for *Oryctolagus cuniculus*, the distribution of which was described earlier (Zagorodniuk, 2023a), as well as for *Equus ferus* and *Ovis gmelini*, the occurrences of which are associated with relatively local centers or places of semi-free keeping and are sufficiently described in the text. The same applies to *Cervus nippon*. For each record, the following information is indicated: location, date of discovery, details of the find (number of individuals and/or biotope), reference to the author of the observation and/or source. We indicate the coordinates in square brackets in cases where we have established them based on information about the find. In some cases, the exact coordinates cannot be established due to the lack of details about the locality, which is indicated separately. All records are grouped by geographic and administrative criteria (e.g., 'northern regions', 'Kyiv Oblast', etc.).

If the source is not a scholarly publication, it is marked with the following abbreviation: *SN – for social network (SN-FB – Facebook; SN-INat – INaturalist; SN-UkrBIN – Ukrainian Biodiversity Information Network; SN-DC-BDU – for 'Data Center Bio-diversity of Ukraine'); *MM – for mass media (MM-NM – for news media; MM-YT – for Youtube); *PC – for personal communication (PC-N – naturalists; PC-B – biologists); * FP – for minor faunal publications. Other abbreviations: NNP – national nature park, AS1a-AS3c – alien statuses (according to the classifier in Zagorodniuk (2023b)), explained below; HG – hunting grounds; AR – autonomous republic; ad. – adult specimen; juv. – juvenile specimen; HE – housing estate; NMNH – National Museum of Natural History, NAS of Ukraine; PLS – private limited company.

When collecting data from open sources, their verification was carried out: on the basis of photos and video materials, descriptions of animals, additional discussions, taking into account the previous experience of respondents and comparison of the received data with confirmed scientific information, the presence of references to analysis by other specialists. Information on specimens transferred to the collections of zoological museums was also used.

It is worth noting that the largest amount of data comes from amateurs (the type of finds designated here as SN-FB and SN-INat). When referring to these sources, the name of the author of the find is indicated. The large volume of data from these resources indicates a significant prevalence of alien species and special attention to them. The fact of receiving a large amount of data precisely from amateurs who often conduct observations near populated areas confirms the opinion that alien species often settle precisely in disturbed (unnatural) biotopes.

General characteristics of the group

The analysis is limited to introduced species whose appearance is associated with human activity, in particular with intentional and accidental introductions and escapes from culture (Table 1). It is based on the 'AS3' group according to our proposed classifier of alien statuses (Zagorodniuk, 2023b). In fact, these are species that appeared not as a result of natural dispersal in the face of climate change, but due to human activity. It does not include species known exclusively in culture (zoos, experimental farms, laboratories), as well as domestic animals and pets, although the latter are known to form feral groups, in particular cows (Zhyla, 2021).

Some of the facts of the appearance (invasion, introduction, expansion) of alien species, as well as the peculiarities of spatial or long-term dynamics of their populations in Ukraine as a whole or in its separate regions, are considered in some works of the authors and our colleagues. Therefore, only summary data important for the formation of a general knowledge system are presented here for such species or regions. The first such review (and list of species) of the mammal fauna of Ukraine was presented in our 2006 review (Zagorodniuk, 2006), followed by further updates of species statuses in the 2012 review (Zagorodniuk & Emelyanov, 2012). Here, the list has been substantially refined and the data detailed.

With the exception of accidental escapes from captivity that do not form local wild populations, i.e. species of the 'marginal' group (subgroup AS1c), all the objects of this study belong to the 'introductions' group (AS3), which includes three subgroups (after Zagorodniuk, 2023b): AS3a – artificially introduced [formerly] native species; AS3b – deliberately introduced alien species; AS3c – introduced or escaped species with a wide expansion. The list of such species in the wild fauna of Ukraine includes 11 nominations, including three species from the superorder Rodentia (European rabbit, muskrat, coypu), three species from the superorder Carnivora (raccoon dog, American mink [vison], northern raccoon), five species from the superorder Ungulata (sika deer, fallow deer, mouflon, onager, wild horse).

Table 1
Features and motives for introducing alien species

Ways of introduction	Examples (more details in the text)
Intentional introductions 1 (hunting ground enrichment programmes)	Planned introductions in hunting grounds; examples include muskrat and raccoon dog in the Kreminna Lakes in the 1960s (Sakhno & Simonov, 1956)
Intentional introductions 2 (non-regular introductions)	Keeping near water bodies and in some cases in a semi-free state - muskrats and coypu (e.g. coypu farm in Oleksandrivka, Donetsk region (our data)
Escapes from captivity	Numerous escapes of the American mink (vison) from fur farms, with the formation of local populations in all regions where fur farms were located (see below); regular escapes of coypu in different regions with the formation of small local groups (see below)
Expansions from introduction or escape sites in other countries	Muskrat in western Ukraine, from the introduction sites in Poland (Tatarynov, 1952); appearance of the American mink in the Kyiv Reservoir from the spontaneous introduction sites in Belarus (Panov, 2002)
Local semi-free rearing with permanent biotechnology	Breeding in hunting farms of enclosure type: sika deer, fallow deer, mouflon (Evtushevsky, 2012)
Releases in the case of the destruction of the keeping system	The devastation of private estates, kennels and menageries in areas of active combat and the destruction of holding facilities or infrastructure with the evacuation of owners provoked by military operations (Zagorodniuk, 2024).

Introduced species in the state survey system

Since 1960, Ukraine has had a state standard for surveying game species, known as state statistics in the form of '2tp-hunting' (Rizun & Bondarenko, 2016; Khoyetskyy, 2017). The document is called 'Report on the survey, harvesting and breeding of game animals' and is mandatory (https://zakon.rada.gov.ua), so such data are important. Some alien mammal species fall into the category of 'game', and therefore are subject to survey at the level of individual farms, administrative districts and oblasts. The final data are organised by oblast and are available for analysis (https://ukrstat.gov.ua).

Such data have some shortcomings related to survey methods and ways of summarising data (e.g. double counting of the same animals during their movements), but they allow us to identify undoubted trends in population changes in space and time. There are many examples of such analyses, e.g. for elk (Khoyetskyy, 2011) and deer (Zagorodniuk, 2022), and there are also examples of analyses of the situation in Ukraine as a whole (e.g. Rizun & Bondarenko, 2016) and in specific regions, e.g. for game animals in the eastern oblasts of Ukraine (Lazariev, 2023a) and for carnivores of the family Mustelidae in Poltava Oblast (Lazariev et al., 2024).

Given the composition of the game fauna (Zagorodniuk & Dykyy, 2012), such statistics do not exclude introductions. Moreover, in a number of cases, they become objects of special attention and breeding as important hunting resources. An example is the sika deer, also known in Ukraine as the 'spotted deer' (Evtushevsky, 2012). In total, the list of game species (28 items) included in the 2tp-hunting tables includes 10 alien species, all of which are introduced species: 1) *Oryctolagus cuniculus*, 2) *Myocastor coypus*; 3) *Ondatra zibethicus*; 4) *Nyctereutes procyonoides*; 5) *Neogale* ('*Mustela*') *vison*; 6) *Equus hemionus*; 7) *Equus ferus*; 8) *Cervus nippon*; 9) *Dama dama*; 10) *Ovis musimon* (=*gmelini*) (Zagorodniuk & Dykyy, 2012: 39). Official statistical information on the population abundances of these species as of 2021 (the last year before the full-scale invasion of Ukraine by the Russian Federation) is presented in Table 2.

The results of the surveys of five species, which are the most complete in the 2tp system, were used to build a map of the distribution and spatial distribution of species numbers within Ukraine. Numbers of coypu are reported in statistics only in certain years, for example, in 2002, 35 individuals of this species were recorded in Donetsk Oblast, and in 2005, 6 individuals were recorded in AR Crimea. Other data for Crimea are also provided for different years: for muskrat, the latest data are available from 2011, and for fallow deer from 2012. For other species, such as the common raccoon dog and mouflon in Crimea, the data are available from 2013 (in subsequent years, statistics are given without taking into account AR Crimea and other occupied territories). Onager was recorded in 2012 in Kherson Oblast (99 individuals) and in 2013 in Mykolaiv Oblast (20 individuals).

Table 2
The numbers of introduced species of the game fauna of Ukraine by oblasts (data for 2021, alphabetical order)*

Oblast	Rodent			Carnivora		Ungulate			
	OrCun	MyCoy	OZib	NyPro	NeVis	CeNip	DaDama	EqFer	OvGme
AR Crimea	–	[6]	[21]	[5]	–	–	[10]	–	[65]
Cherkasy	–	–	4455	332	0	794	100	–	160
Chernihiv	–	–	6407	1714	2053	55	0	–	0
Chernivtsi	–	–	1114	0	0	0	45	–	0
Dnipropetrovsk	–	–	1378	426	0	0	0	–	0
Donetsk	–	[35]	581	298	264	90	0	–	0
Ivano–Frankivsk	–	–	962	0	0	44	75	–	13
Kharkiv	–	–	10	1074	2616	466	34	–	0
Kherson	–	–	720	429	0	0	310	[99]	251
Khmelnytskyi	–	–	13922	78	187	197	0	–	0
Kirovohrad	–	–	6419	475	0	121	40	–	0
Kyiv	–	–	2229	311	49	107	146	–	110
Luhansk	–	–	1215	434	93	95	0	–	0
Lviv	–	–	4406	78	0	32	8	–	0
Mykolaiv	–	–	17	62	0	0	0	[20]	0
Odesa	[75]	–	5810	90	0	74	0	–	0
Poltava	[14]	–	6220	1107	65	725	151	–	115
Rivne	–	–	3780	631	1584	190	139	–	92
Sumy	–	–	9441	1129	0	75	0	–	0
Ternopil	–	–	12809	0	0	71	10	–	0
Vinnytsia	–	–	8066	0	0	535	150	–	66
Volyn	–	–	3596	812	798	798	10	–	0
Zakarpattia	–	–	703	0	0	0	148	–	0
Zaporizhzhia	22	–	0	293	0	0	0	–	0
Zhytomyr	–	–	2812	793	1605	232	3	–	0
Cartographic analysis	–	–	Fig. 3	Fig. 6	Fig. 7	Fig. 10	Fig. 13	–	Fig. 14

Note: * – species designations are given by acronyms of the first two letters of the genus and the first three letters of the species name; '0' means the specified zero number, a dash ('–') means that there are no records of this species in the statistics for 2021; values in square brackets refer to one of the previous years (since no data were available in 2021) and relevant comments on such data are provided in the text further.

Table 3
Introduced species and their status categories

Species	Initial category	Current category and trends	Species	Initial category	Current category and trends
Oryctolagus cuniculus	AS3b	AS3b + AS1c → AS3c	*Equus ferus*	AS3a	AS3a [+ AS3a → AS3c]
Ondatra zibethicus	AS1c	AS1c + AS1b	*Equus hemionus*	AS3a	AS3a
Myocastor coypus	AS3b	AS3b + AS3c	*Cervus nippon*	AS3b	AS3b [+ AS1c → AS3b]
Nyctereutes procyonoides	AS3b	AS3b + AS3c	*Dama dama*	AS3b	AS3b [+ AS1c → AS3b]
Neogale vison	AS3c	AS3c + AS1c → AS3c	*Ovis gmelini*	AS3b	AS3b [+ AS3b → AS3c]
Procyon lotor	AS1c	AS1c [AS1c → AS3c]			

Annotated list of introduced species

In total, there are 11 such species, and all of them represent the game fauna, i.e. they have or had obvious economic value at the time of introduction or cultivation. The data are summarised in Table 1. Subspecies are not considered here (e.g. Russian red tree squirrel), as well as hybrids, including the so-called 'Askanian deer', which is a complex hybrid of many forms of the genus *Cervus* (Volokh, 2021), as well as hybrid or feral populations of cats, pigs and other animals. No examples of domesticated animals are given, although such facts are important (e.g. feral cattle).

1. *Oryctolagus cuniculus* (Linnaeus, 1758) (European rabbit). Status – AS3b (AS3b + AS1c → AS3c). A mammal species from the family Leporidae of the order Leporiformes (Lagomorpha auct.).

An introduced species with exclusively local expansions around the introduction sites, which resulted in the formation of a mosaic range. In total, about 10–15 points of introduction are known, mostly in the southern regions of Ukraine (Fig. 1b). The introduction is analysed in several special articles (Zagorodniuk, 2023a). In the statistical reporting of '2tp-hunting', this species has been recorded in the southern oblasts of Ukraine since 1992 and early 2000s, particularly in Crimea (1992–1994), in Kherson Oblast until 2006, and in Odesa Oblast until 2012 (until 2006, the species was distributed in hunting grounds of Odesa Oblast). In some years, the species was also recorded in Mykolaiv Oblast (Fig. 1a). In the western oblasts of Ukraine, the introductions of the mammal were carried out in 2006–2011, but without the formation of stable natural populations. From 2006 to 2008, the species was recorded in Zakarpattia Oblast (33–69 individuals). In 2010, data on the number of 112 individuals in Chernivtsi Oblast were provided, but there are no data about population in this oblast in subsequent years. In 2001, 10 individuals were relocated to Lviv Oblast, but the fate of the animals in subsequent years is also unknown.

In Zaporizhzhia Oblast, the species has been recorded since 2008 'until now' – there are data on the number of 22 individuals as of 2021 and a downward trend in numbers during 2019–2021 (during these two years, the number decreased from 264 to 22 individuals, probably the population has reached extinction). A detailed example of the emergence and extinction of one of the local populations was recently described for Podillia (Vikyrchak & Bachynskyi, 2019). Over the past 10 years, there have probably been attempts to disperse the species in Poltava Oblast (statistics show a population of 14 individuals in this region), but in subsequent years, according to statistics, the species has not been recorded in Poltava Oblast, and dispersal has not led to the formation of a population. An analysis of all the data showed a complete extinction of most populations since the early

1980s (Zagorodniuk, 2023a), most likely due to the spread of myxomatosis. Some essentially artificially maintained settlements have survived near Odesa, on the slopes of coastal estuaries. It is also known that there are separate nurseries that regularly sell European rabbits to form local (essentially garden-type) settlements. One of these was at the 'Mezhyhirya' Residence near Kyiv (ibid.). In general, the area of relatively successful (or temporarily successful) introductions covers only the steppe zone, primarily the southernmost coastal regions (Fig. 1b).

The example of this introduction shows that a successful and long-term introduction with the formation of stable and highly abundant populations (colonies) can result in a complete fiasco due to the emergence of alien (zoonosis) infections (Zagorodniuk, 2023a). In addition, the species did not disperse over long distances and therefore did not create a metapopulation system, i.e. it was represented by essentially completely isolated settlements tied to the places of initial introduction. That is why it had no adaptations to dispersal and the formation of an integral range, as well as no compensatory mechanisms to support some local settlements through arrival of migrants from others, which would maintain outbreeding and population levels.

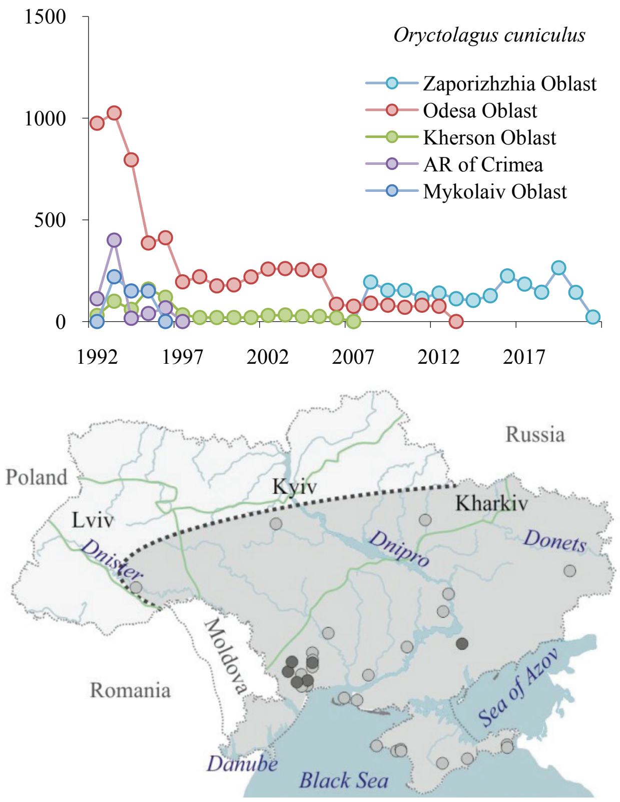

Fig. 1. Population of *Oryctolagus cuniculus* according to hunting statistics in selected oblasts of Ukraine where relatively long-lived populations were recorded (*a*) and the distribution of colonies of this species in Ukraine (*b*) in the second half of the 20th century and early 21st century (based on data from Zagorodniuk (2023a)): light colours indicate the sites of introductions where populations had disappeared before the end of the 20th century, dark colours indicate locations where rabbits have been known until recently

2. *Ondatra zibethicus* (Linnaeus, 1766) (muskrat). Status – AS3b (+AS1c → AS3c). A mammal species from the family Cricetidae of the order Muriformes (Rodentia auct.).

An alien mammal species that appeared in the fauna of Ukraine as a result of dispersal (Panov, 2002). One of the first introduction attempts was the release of 36 individuals at a pond in Kharkiv Oblast in 1929, where the animals did not survive. Large-scale efforts to disperse the species, which resulted in the first natural populations of muskrats in Ukraine, were carried out in 1944–1947. The southern and eastern regions of Ukraine became one of the first areas of introduction of the species, where animals selected in Arkhangelsk and Kurgan oblasts were released (Kolosov & Lavrov, 1968; Volokh, 2002), while in Lviv Oblast the species probably appeared as a result of expansion from Poland, as the first known habitats of muskrats in Lviv Oblast were the areas of the Shklo River and the Bolozivka River near the Ukrainian-Polish border (Tatarynov, 1952). In northern and western regions of Ukraine, the resettlement work continued until the 1950s and 1960s.

Due to their high fecundity and ability to rapidly expand their range, by the 1970s muskrats had rapidly occupied almost all river systems in all regions of Ukraine, and by the 1980s had settled in all major rivers and most other water bodies in the Azov Sea region (Volokh, 2002). Nationwide, muskrat numbers peaked in the early 2000s and have been at their highest since 1998. Since 2012 there has been a gradual decline, but now the number has somewhat stabilised and fluctuates between 102–138 thousand individuals (Fig. 2). A similar situation with the dynamics of this species is observed in Poland, but the phenomena of increase, peak, further decline and stabilisation in this country occurred earlier (probably due to the earlier introduction in Poland than in Ukraine): the population of the species rapidly decreased, at least in the period from 1991 to 2012, after which it stabilised (Dziech et al., 2023).

According to the results of the analysis of the population by regions (Fig. 2b), as of 2021, the population decreased in the eastern and southern regions of Ukraine (most of these regions are those where the animals appeared much earlier than in the western and southern oblasts). Another factor contributing to the low level of muskrat population in the steppe and forest-steppe regions of Ukraine is the instability of the hydrological regime of rivers and other water bodies in these natural areas. For example, a decline in muskrat population and the absence of registration of this species in some areas is noted in Kharkiv Oblast (according to hunters), mainly in places where swamps are drying up. The population of muskrats has also decreased in Sumy Oblast (according to local residents, PC–B: S. Panchenko). In these regions, in particular in the eastern regions, there was a peak in population growth (Lazariev, 2023a), which is typical for most alien species when they enter new habitats.

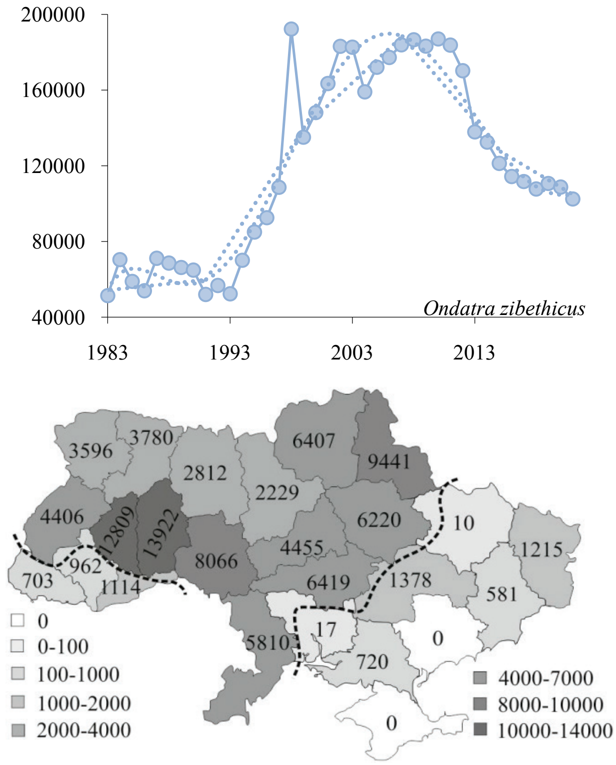

Fig. 2. Population of *Ondatra zibethicus* in Ukraine according to statistics for the period from 1983 to 2021: long-term population dynamics (*a*) and distribution of data by oblasts as of 2021 (*b*): the dashed line indicates the areas with the lowest numbers

High populations as of 2021 are given for Ternopil and Khmelnytskyi oblasts. The release of muskrat in these regions took place later, in the 1950s and 1960s, and the volume of introduction activities in these oblasts was ten times lower (fewer releases and number of released animals) compared to other regions of Ukraine (Kolosov & Lavrov, 1968), so it is likely that the process of expansion of the species in the region continued later than in most other regions, but the animals are well established and now the level of abundance in these regions is also beginning to stabilise after the transition from peak levels of abundance. In general, the higher numbers in the western part of Ukraine are explained by the greater stability of the hydrological regime of the water bodies in which the animals live and the higher productivity of the ecosystems.

Despite the statistical data indicating low numbers of the species in the steppe area, including the alleged absence of muskrats in Zaporizhzhia Oblast, it is known that the species exists in this region (Volokh, 2002) and occurs in different parts of the oblast. The prevalence of muskrats in Zaporizhzhia Oblast is also evidenced by the collection of muskrat specimens (n = 63) from the territory of Veselivka rural council, collected during 2005–2011 by N. Lebedeva and transferred to the NMNHU (materials processed by the authors). In addition, muskrat finds are also known from the territory of Crimea. Data on actual findings confirming the presence of muskrats in Zaporizhzhia Oblast and Crimea are presented:

* Zaporizhzhia Oblast, Khortytsia island [47.836163, 35.085676], n = 1, 12.02.23 (SN-FB: Khortytsia National Reserve); * Zaporizhzhia Oblast, Yakymivka Raion, 46.505847, 35.121144, n = 1, 31.03.21 (SN-INat: G. Mykytynets); * Zaporizhzhia Oblast, Zaporizhzhia, Osypenko residential area, [47.881871, 35.024478], n = 1, 2023, the animal was walking along the sidewalk, next to the River Verkhnia Khortytsia (MM-NM: Holos Zaporizhzhia); * Zaporizhzhia Oblast, eastern outskirts of the Enerhodar, canal from the Dnipro River, regular findings in 2010–2020 (PC: Y. Shorokhova); * AR of Crimea, Bilohirsk Raion, Simiane, 45.459984, 34.762471, n = 1, 13.05.23 (SN-INat: T. Bediev).

Based on the data on the distribution of this species, it can be stated that muskrats are found in all oblasts and the Autonomous Republic of Crimea, but there has been an obvious decrease in population, mainly in the eastern and southern regions, which is likely due to the instability of the hydrological regime: drying up of swamps and changes in water levels in artificial reservoirs, regulation of water levels in rivers, which is critical for the life of these animals. In the western and northern regions, the number of muskrats is higher, which may be due to better hydrological conditions, ecosystem productivity, and the difference in the time of introduction and population formation between these groups of regions. A decline and stabilisation of muskrat numbers in the north-western regions of Ukraine can be expected over the next decades.

3. *Myocastor coypus* (Molina, 1782) (Coypu). Status – AS1c (+ AS1b). A mammal species from the family Echimyidae of the order Muriformes (Rodentia auct.).

This alien species was introduced to Ukraine in 1948 in the amount of 60 individuals for semi-free keeping in the Lower Dnipro region, and breeding of these animals proved to be quite productive (Kolosov & Lavrov, 1968). The history of the taxonomy is rather confusing, with the first reviews designating the species as *Myopotamus coypus*, noting that the species was initially known only in the Lower Dnipro, where it had been kept in a semi-free state in the Lower Dnipro Muskrat Farm since 1949 (Tatarynov, 1956: 162), and during 1950–1953 coypu farms were established in a number of other regions, including Lviv Oblast (farms in Horodok and Sokal raions), Volyn Oblast (Olyka and Rozhany raions), and Rivne Oblast (Dubno farm) (Tatarynov, 1956).

Currently, coypu is classified in the genus *Myocastor* (from the 1965 review onwards) and is considered to be part of the family Echimyidae (Galewski et al., 2005; Zagorodniuk & Kharchuk, 2022). In recent years, there have been many reports of the species being found in nature, which indicate obvious changes in nature and a significant distribution of the species in natural ecosystems of all natural zones (Zagorodniuk, 2006). Several factors contributed to this: climate warming, a decline in demand for the fur of semi-aquatic animals, the decline of fur farms, etc.

The resistance of coypu to winters and frosts was first noted in a review by Tatarynov (1956). There have been reports of escapes or deliberate releases of animals into natural habitats and their existence in the wild during warm or even winter periods, in particular in winter in the water bodies of Luhansk Oblast (Lazariev, 2023a). The animals have been successfully surviving the winter, especially in recent years, not only due to warming, but also due to frequent cases of human care by people who feed them. Coypu do not prepare food for the winter on their own, so feeding is critical to their survival. We have previously described coypu sightings in the wild in Eastern Ukraine (Lazariev, 2023a). Information on coypu findings in natural ecosystems of other regions of Ukraine is presented in the format of a cadastre.

Fig. 3. Finds of coypu: (*a*) general view of the canal on the territory of the Kalynova Sloboda housing estate, Krykhivtsi, Ivano-Frankivsk Oblast, March 2018 (photo by N. Smirnov); (*b*) animals living in this place (photo by N. Smirnov); (*c*) distribution map of the species based on the finds described in the text; light colours indicate single records, dark colours – regular occurrences

In total, more than 50 records of coypu were collected throughout Ukraine, mostly based on the analysis of the most popular open sources on biodiversity, where 42 records indicated single finds and 13 records indicated finds where the long-term existence of these animals (more than 2 years) was registered. We also found the presence of coypu specimens in the collections of the Zoology Department of the National Museum of Natural History (Kyiv), which were found in the wild (No. 12524, details in the cadastre). Due to the considerable amount of such data, we present in full only information on the long-term existence of coypu in floodplain habitats, and single finds are noted one for each region from which we know of such finds.

Information on the long-term existence in floodplain habitats. Western oblasts. * Lviv Oblast, Lviv Raion, Shchyretst, 49.647256, 23.859956, n = 5: 1 ad., 4 juv., 23.03.23 (SN-FB: A. Aftanas); * Lviv Oblast, Shchyrets reservoir, 10 km to the south of Lviv, Shchyrka River, 49.741225, 23.942480, n = 2, 30.09.22, observed for three years (PC: V. Koreniuk); * Ivano-Frankivsk Oblast, Krykhivtsi, canal on the territory of HE 'Kalynova sloboda', 48.904976, 24.668631 (Fig. 3), 2018–2021, the finding of coypu has been recorded continuously during this period, with about 30 individuals of different ages (ad. and juv.) and different colour variations (dark and light) living here, fed by local residents (PC-B: N. Smirnov); * Chernivtsi Oblast, Vyzhnytsia Raion, Lake near Banyliv, 48.376362, 25.356387, n = 30, 30.02.21 (ad. and juv.), introduced in 2018–2019 pp., fed by local residents (I. Skilsky (PC-B), based on PC: N. Kyrychenko); * Chernivtsi Oblast, Banyliv, 48.375622, 25.355628, 24.10.20, at the time of the finding, the coypus had been in this place for about 10 years, fed by local residents (PC-B: I. Skilsky).

Eastern oblasts. * Dnipropetrovsk Oblast, Dnipro city, 48.495208, 35.032953, inland port, 4.11.22 (PC-B: H. Zadorozhna), there have been findings in this place continuously for several years (SN-FB); * Poltava Oblast, Poltava, Vorskla River, 49.566083, 34.592442, n = 8, 16.12.21, these animals were fed by local residents. In October 2021, a litter of 6 individuals (MM-NM: "IRT Poltava"); * Luhansk Oblast, Striltsivsky Steppe, Cherepakha River [49.302634, 40.090371], n = 1, 1982, coypu was observed in summer and winter, even after ice formation (Chronicles of the Nature of the Luhansk Natural Reserve 2004); * Donetsk Oblast, Oleksandrivka rural settlement, 48.969719, 32.248130, 1990, recording regular findings of coypu in nature through escapes from the farm (PC-B: O. Reznik); * Luhansk Oblast, Sievierodonetsk, Parkove lake, 48.961043, 38.481127, n = 1, 29.01.21, albino (MM-NM); * Zaporizhzhia Oblast, 47.886682, 35.089935, Zaporizhzhya city yacht club, 2022 (MM-YT).

Southern regions. * AR of Crimea, northern outskirts Luchyste, floodplain Demerdzhi River, 44.749077, 34.387722, six findings in 2021–2024 (SN-INat: S. Bogdanovich); * AR of Crimea, Yalta Raion, 44.697074, 34.349258, neighbourhood Izobilne, five findings in 2021–2022 (SN-INat: S. Bogdanovich); * AR Crimea, Dzhankoi Raion, neighbourhood Ostrovsk, Syvash bay, n = 1, 19.08.93, Peklo A. (Collection of the National Museum of Natural History at the NAS of Ukraine: No. 12524, skin, female, juv.).

Single findings. Western oblasts. * Khmelnytskyi Oblast, southern Khmelnytskyi, 49.387533, 26.984089, n = 1, 20.09.18, (SN-FB: V. Demtsun); * Chernivtsi Oblast, Novoselytsia Raion, Boiany, 48.305377, 26.121576, Boiany village, 1.10.22 (PC-B: I. Skilsky); * Rivne Oblast, Kruhle village, 50.619354, 26.342552, n = 1, 1.10.22 (SN-INat: O. Havryliuk); * Vinnytsia Oblast, Pohrebyshche city, Zavodsky pond, 49.493824, 29.264668, n = 1, 10.06.21 (SN:UkrBIN: K. Pogorila). Central oblasts: * Cherkasy Oblast, Talne Raion, Kobrynova Hreblia [48.968020, 30.719216], 15.06.18, domestic coypu, for several weeks, it fed in villagers' gardens (MM-NM: 'Visti Cherkashchyna'); * Kyiv Oblast, Hrebinky, Protoka River, 49.961496, 30.185469, n = 1, 3.07.22 (SN-INat: O. Uhnivenko); * Chernihiv Oblast, Nosivka Raion, Volodkova Divytsia, 50.944, 31.789, n = 1, 25.12.97 (PC-B: B. Kedrov). Eastern oblasts: * Donetsk Oblast, Donetsk, Bahrationa street [47.993183, 37.895537], n = 1, 17.04.23 (MM-NM); * Kharkiv Oblast, Kharkiv, Studenok River [49.925579, 36.379871], n = 1, 28.08.21, (SN-B: I. Kozytskyi); * Dnipropetrovsk Oblast, Dnipro, Monastyrskyi Island [48.461397, 35.079383], n = 1, 12.12.21 (SN-FB: D. Vasilieva); * Sumy Oblast, Lebedyn Raion, 50.63347, 34.287433, n = 1, 5.08.16 (SN-INat: V. Parkhomenko).

4. *Nyctereutes procyonoides* (Gray, 1834) (Raccoon dog). Status – AS3b + AS3c. A mammal species from the family Canidae of the order Caniformes (Carnivora auct.). The species was introduced in Ukraine in 1928, when it was first released in Poltava Oblast. More active work on the species' introduction began in 1935–1936, when the species was released in the eastern oblasts of Ukraine and Kyiv Oblast. In some oblasts of the centre and south, the work continued until 1941. In the post-war years, the introduction of the species was resumed in the western oblasts and this process lasted at least until 1952 (Kolosov & Lavrov, 1968).

As of 2021, the animals are not recorded in official statistics in Vinnytsia, Zakarpattia, Ivano-Frankivsk, Ternopil, and Chernivtsi oblasts. Low numbers are recorded in Lviv, Mykolaiv, Odesa, and Khmelnytskyi oblasts (less than 100 individuals). As of 2013, the species was introduced in the Crimea, where 8 individuals were released. The total number of animals of this species in the Crimea as of the same year was 5 individuals (Table 2).

The population dynamics of *Nyctereutes procyonoides* is wave-like with fluctuations occurring every 5–10 years (Fig. 4a), and generally shows an increase during the 1990s and stabilisation of the population dynamics during the 2000s.

The analysis of the population of common raccoon dog by regions as of 2021 showed that the species is absent or scarce in mountainous areas. Average numbers are typical for the eastern, southern, and central regions, and the highest numbers are recorded in the southern regions (Fig. 4b). The positive dynamics of the common raccoon dog population is probably related to its unpretentiousness in terms of prey and its special position in the guild with *Vulpes vulpes*, *Canis lupus* and *C. aureus*, where the latter two species have low distribution and abundance.

The species is distributed in the northern oblasts of Ukraine. The largest numbers according to hunting statistics are recorded in Chernihiv, Sumy, Kharkiv and Poltava oblasts, with average numbers in the central, southern and eastern regions, but the species is scarce or absent in the mountainous and adjacent oblasts (Fig. 4b), despite the fact that animals were released in these oblasts in the 1950s (Kolosov & Lavrov, 1968). However, there are reports of sightings of the species on the edge of its range, close to the borders of Ternopil and Zakarpattia oblasts, and isolated records in regions where, according to statistical data, no animals of this species have been recorded. Below are some data confirming the presence of the species in some western oblasts and the process of its population spreading to new territories:

* Lviv Oblast, Zolochiv Raion, Peniaky, Northern Podillia NNP, 49.8717, 25.1789, n = 1, 22.03.22 (SN-DC-BDU); * Lviv Oblast, 49.006, 23.21 (FP: Martsiv et al. 2021); * Vinnytsia Oblast, Stepanivka, 49.131474, 28.765112, 27.08.05, without detailed information (FP: Matviichuk, 2015); * Vinnytsia Oblast, Zhmerynka Raion [49.018790, 28.050039], n = 1, 29.10.15, an animal that fell under a combine harvester was placed in an enclosure (MM-YT: TV channel VITA); * Zakarpattia Oblast, Uzh NNP [49.002181, 22.675141], n = 1, 22.09.23, rescued from dogs by the park protection service (MM-NM: mukachevo.net based on the materials of the Uzh NNP).

Despite the absence of records in the 2tp statistics in a number of regions, the common raccoon dog occurs in both Zakarpattia and Vinnytsia oblasts, but is not abundant there. This is also confirmed by the dynamics of the species' population decline in the oblasts from the north-east to the south-west. There is also a continuation of expansion to new regions where the species was not present or had not been recorded for a long time, such as in the Uzhanskyi NNP. In general, despite its low distribution in the steppe, forest-steppe and mountainous areas of Ukraine, the species continues to increase in number and to expand, although these processes are not rapid.

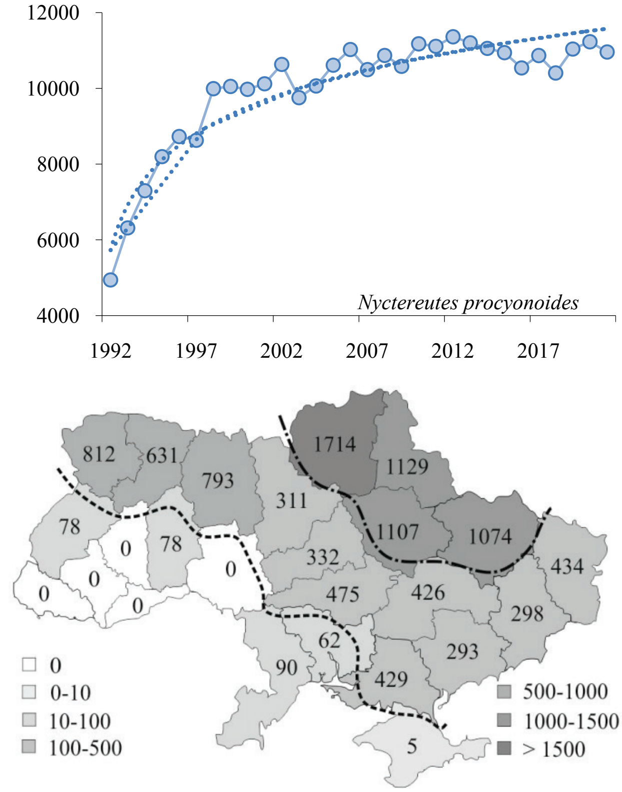

Fig. 4. Population of *Nyctereutes procyonoides* in Ukraine according to hunting statistics from 1992 to 2021: long-term dynamics of abundance (*a*) and distribution of data by oblasts as of 2021 (*b*); the dashed line indicates the areas with minimum and maximum numbers

5. *Neogale vison* (Schreber, 1777) (American mink). Status – AS3c (in the future AS1c → AS3c). A mammal species from the family Mustelidae of the order Caniformes (Carnivora auct.). This species appeared in the fauna of Ukraine as a result of the creation of farms for its breeding as a valuable fur animal and subsequent escapes from culture during the 1950s, and as a result – the formation of natural populations. Thus, in the 1960s, the species was observed in Chernihiv Oblast, and in the 1980s, animals were already found in the Kyiv and Kremenchuk reservoirs, but it is known that animals brought from Belarus were deliberately released in the Kyiv reservoir (Panov, 2002). The Belarusian population, which is the source for the populations in Ukraine, is quite abundant and accumulates significant morphological variability, which is the subject of special attention (Savarin, 2023).

Official statistics indicate that populations of this species as of 2021 are concentrated in regions directly related to the areas of introduction (Fig. 5b), namely in the central and northern regions (Zhytomyr, Kyiv, Chernihiv oblasts), in the western oblasts connected by rivers to the northern oblasts (Volyn, Rivne, Khmelnytskyi oblasts) and in eastern Ukraine (Donetsk, Luhansk, Poltava, Poltava, Khmelnytskyi oblasts), in the western oblasts connected by river basin with the northern regions (Volyn, Rivne, Khmelnytskyi oblasts) and in eastern Ukraine (Donetsk, Luhansk, Poltava, Kharkiv oblasts), and no new introductions are currently known. The rate of expansion of this species was not as high as in the case of other alien species, such as *Ondatra zibethicus*.

The species is absent in most southern and western regions of Ukraine, which is confirmed by literature data. *Neogale vison* has not yet migrated to the lower reaches of the Dnipro River and has not been recorded in Dnipropetrovsk Oblast (Bulakhov & Pakhomov, 2006), and the species' distribution depends on the river basin. For example, the bulk of finds in Donetsk Oblast were from the northern areas of the Siversky Donets basin (Lazariev, 2023a).

The majority of *Neogale vison* records published in social networks and databases (GBIF) coincide with the range we have outlined based on statistical data (Fig. 5b). There may have been errors in the species record system, given the confusion in species identification and designation in statistical reporting (Zagorodniuk & Dykyy, 2012). In order to clarify the locations of the species in the regions where the absence of animals is indicated by statistical data, data on actual findings in the areas of the southern limit of the range within Ukraine are presented below. Several records were reported from Vinnytsia Oblast, though mostly only from its northwestern regions. The species is also recorded in Sumy Oblast, despite the absence of these data in official statistics.

* Vinnytsia Oblast, Vinnytsia Raion, 49.230988, 28.364263, n = 1, 25.03.20, a mink crossed the dirt road (SN-INat: O. Zmurko); * Vinnytsia Oblast, Lityn Raion, 49.255847, 28.091536, n = 1, 16.03.20, in the thickets of phragmites (SN-INat: O. Zmurko); * Sumy Oblast, Desna-Stara Huta NNP, floodplain of Desna River [52.315019, 33.402435], n = 1, 4.10.19, river bank (SN-FB: S. Hlushchenko); * Sumy Oblast, Krolevets [51.548016, 33.404445], n = 1, 26.09.21, a dead individual on the shore of a lake (SN-FB: A. Kovtun).

Until 2011, the results of the *Neogale vison* and *Mustela lutreola* population surveys were reported as data on the number of a single species called 'free mink'. Since 2011, the numbers of these two species have been recorded separately. It is obvious that even before 2011, *N. vison* clearly accounted for the largest share of the total number of 'free mink' in the survey data. The whole sum of publications (Panov, 2002; Rozhenko, 2015; Lazariev, 2023a etc.) and reports on 'minks' in museum collections indicate an extremely low number of *M. lutreola*, proving the fact that *N. vison* accounted for a larger proportion of the total number of free-ranging mink. That is, the population of the European mink was lower than that of the American mink during the period of their monitoring from 1983 to 2021. From the available data, it can be shown that as of 2011, the percentage ratio of *N. vison* to *M. lutreola* in the total number of these two species was 75.1% to 24.9%, respectively. In ten years (as of 2021), these figures have changed by 10% in favour of *N. vison* (85.2%/14.8%, Fig. 5a). The population dynamics of this species shows a constant and rapid increase in numbers throughout the entire period of recording of this species, from 1983 to 2018. In 2018, this estimate reached a maximum of 11 436 individuals, after which there was a slight decline in numbers and as of 2021, the figures decreased to 9 998 individuals (Fig. 5a).

In previous reviews of the spread of alien species, it was found that expansion continues, at least in the eastern regions (Lazariev, 2023a). Also, based on the data obtained on detections and population dynamics, it can be assumed that the expansion of the species is occurring in the entire Ukrainian part of its range and that it may occupy new regions of Ukraine in the near future.

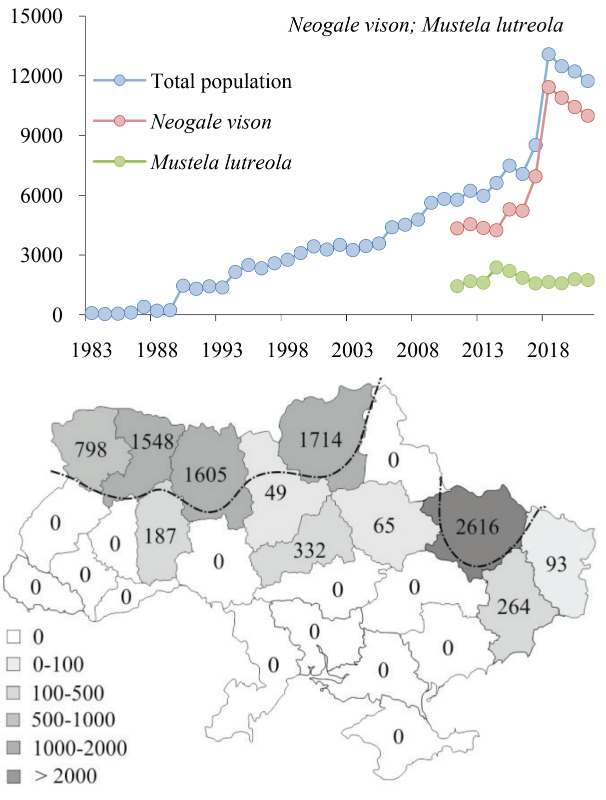

Fig. 5. *Neogale vison* and *Mustela lutreola* in Ukraine according to hunting statistics from 1983 to 2021: long-term dynamics of population (*a*) and distribution of *N. vison* population data by regions as of 2021 (*b*); the dashed line indicates the regions with high abundance

6. *Procyon lotor* Linnaeus, 1758 (raccoon). Status – AS1c (in the future AS1c → AS3c).

A mammal species from the family Procyonidae of the order Caniformes (Carnivora auct.). It occurs in the Palaearctic, where it is an alien mammal species. There are reports of animals found in the natural environment in the neighbouring countries of Ukraine, but there are a number of reports of these animals found in Ukraine during the 2000s, which indicate the possibility of the formation of natural populations of the species in the natural environment in Ukraine (Nikolaichuk & Zagorodniuk, 2019). Earlier introductions of the species in Polissia, on the border with Ukraine (Gomel Region, Belarus) in 1954 and subsequent years, seemed to be successful at the first stages, but by the turn of the 20th and 21st centuries, reliable records of the species disappeared (Savarin, 2007). Today, the species is reoccupying Polissia and is not only extending its range from culture, but also through natural expansion. For example, *P. lotor* is now recorded in Nalibotska Pushcha (70 km from Minsk, 25.08.2023, camera trap), where habitats are favourable for the species (150–200-year-old broadleaf forests) (MM-YT). The number of raccoon sightings is also increasing in other territories adjacent to Ukraine, in particular in Hungary (Schally et al., 2024) and Poland (Dziech et al., 2023), where the species is increasingly approaching the border with Ukraine, in particular, the number of sightings in the regions of Poland neighbouring Ukraine is increasing (Okarma et al., 2012).

Surveys of different groups of nature users confirm that these species are often confused with *Nyctereutes procyonoides*, including due to confusion in naming (Zagorodniuk & Dykyy, 2012). This species is in the earliest stages of introduction in Ukraine, and the area of introduction is generally defined by the proximity of large cities and likely breeding premises that supply the pet market, and all of these are peripheral areas of the country close to the border zones. There is no clear connection with biogeographical zones. However, there is a certain correspondence with the zone of war impact 'E', or, more broadly, 'C+D+E' (after Zagorodniuk, 2024: Fig. 4).

Fig. 6. Map of Ukraine showing record localities of raccoons (*Procyon lotor*) in the wild and the designation of Zone E as an area subject to relatively short-term military intervention (Zagorodniuk, 2024)

Obviously, we can expect new findings in these zones, which will probably be facilitated by frequent cases (according to MM & SN) of keeping of raccoons by the military, as well as the emergence (as a result of hostilities) of evacuation zones where the probability of raccoons escaping into the wild is extremely high. A noteworthy result of the mapping (Fig. 6) is the autonomy of the introduction zone from the expansion zones that are approaching from the west (Salgado, 2018; Stope, 2023) and whose appearance we predicted from the west (Nikolaichuk & Zagorodniuk, 2019). In each case, the main factor in population formation is escape from the captivity, i.e. similar to the situation in Europe. Examples of recent actual records are as follows (Fig. 6):

North (Dnipro Ukraine). * Kyiv Oblast, Vyshhorod Raion, Strakholissia, September 2003, islands on the Dnipro River, 51.123233, 30.464953, n = 2, raccoons came to the tents in search of food (PC-N: O. Bondarenko); * Kyiv Oblast, Kyiv, Sviatoshynskyi District [50.460982, 30.380357], n = 1, winter-spring 2011, The animal was observed twice, in winter and spring in natural (urban) environments, near the bird feeder on the 5th floor of the building and also moved through the trees (Nikolaichuk & Zagorodniuk, 2019); * Chernihiv Oblast, north-eastern raions, borderland, n = 3, summer 2022, near a military field camp, without details about the location, volunteer messages (Zagorodniuk, 2024, with clarification); * Chernihiv Oblast, 'Mykolaivka' border crossing, n = 1, February 2018 (unverified finding, according to bbc.com); * Kyiv Oblast, Yasnohorodka [50.368309, 30.032461], after the bombardment of a farm, animals went outside the territory, including raccoon (SN: message from 3.04.2022); * Kyiv Oblast, between the villages of Dubechnia and Pirnove [50.742229, 30.661193], n = 1, finding in the gazebo, around 2022, escaped pet, was not afraid of people (SN).

Eastern oblasts. * Luhansk Oblast, Sorokyne Raion [48.370511, 39.619898], n = 7, summer 2017, escape from breeding grounds in Samsonivka; * Luhansk Oblast, the outskirts of Kosiora [48.535555, 39.262441], escape of 5 individuals, autumn 2017 (reporting to colleagues: Nikolaichuk & Zagorodniuk, 2019); * Donetsk Oblast, the outskirts of Bakhmut [48.572451, 37.959569], n = 6, summer 2022, in a dugout, videos and messages from the military and volunteers (Zagorodniuk, 2024; more details here); * Dnipropetrovsk Oblast, Doslidne [48.384975, 35.033361], n = 1, 18.06.2017, the animal was removed from a tree by the SES of Ukraine, and handed over to the staff of the 'Pegas' animal shelter, probably an escaped pet (MM-NM: newspaper 'News Kamenskoe'); * Zaporizhzhia Oblast, approximate location: north-eastern part of the oblast, n = 1, 7.02.2023, an animal lives in a dugout at the positions of the Ukrainian military, without details about the exact location (MM).

South. * AR of Crimea, Kerch [45.390370, 36.632783], n = 1, 16.10.2015, an escaped pet, found by local residents and returned to the owners of the ostrich farm from which the raccoon escaped (MM).

7. *Equus ferus* (Boddaert, 1785) (wild horse). Status – AS3a. A mammal species from the family Equidae of the order Equiformes (Perissodactyla auct.).

This ungulate species is extinct in the wild, but domesticated forms have been introduced in a number of regions, including the Przewalski's horse (*Equus ferus przewalskii*) in the Chernobyl Exclusion Zone (Gashchak & Paskevich, 2019). Wild or semi-wild herds of the domestic horse (*Equus caballus*) have been established on Byriuchyi Island, on Tendra in the Black Sea Biosphere Reserve (Selyunina & Chernyakov, 2022), in the Khomutovsky Steppe Reserve and at stud farms in Luhansk Oblast (Fomin, 2023).

In 1998, the Askania-Nova Biosphere Reserve developed a programme to create a free population of Przewalski's horses in the Chernobyl Exclusion Zone. In 1998–1999, 31 individuals of this species were transported (in several batches) to the newly constructed temporary rehoming centre. In January 2004, three stallions from the Kyiv Zoo were brought to the Chernobyl Exclusion Zone, and in September 2004, 10 horses from the Odesa Zoo. In both cases, the animals were released without first being prepared for this in acclimatisation enclosures, and all of them died within a year. Animals brought to the Zone from the Askania-Nova Biosphere Reserve were released into the wild after wintering and in the following years quickly settled in the territory. As of 2003–2004, 65 individuals were recorded in the Chernobyl Zone (Yasynetska & Zvegintsova, 2013).

The main reasons for the decline were anthropogenic factors, including poaching. In 2007 and 2010, some of the animals crossed the Ukrainian-Belarusian border and ended up in the Polesie State Radioecological Reserve. Some of these horses remained in the reserve and bred. As of 2013, the state of the population in Polissia was assessed positively (Yasynetska & Zvegintsova, 2013). Already in 2018, 137 individuals were recorded in the Chernobyl Zone, i.e. the population has increased 7 times in 20 years, although the increase in the last 10 years was 1.5 times less than that in the first 10 years after the introduction (Gashchak, & Paskevich, 2019). Over the past 25 years, wild horses have organically integrated into the native communities of the Central Polissian ungulates and become an integral part of them.

Wild horses prefer to live in forests and, in adverse weather conditions, in abandoned farm buildings (SN). Danger from mines has been a negative factor for the population as a result of hostilities since the beginning of 2022, with one animal killed by a mine explosion (State Border Guard Service of Ukraine data published in MM-NM: Kyivshchyna 24/7). In addition, as a result of forest fires in the exclusion zone, significant areas of forest, which are the main habitat of this species, may be destroyed.

8. *Equus hemionus* Pallas, 1775 (onager). Status – AS3a. A mammal species from the family Equidae of the order Equiformes (Perissodactyla auct.).

This introduced species, like the wild horse, has a special status, in fact, it is a reintroduced species that is being restored in Ukraine. This species was found in Ukraine in historical times, in the steppe (coastal) regions (Sokur, 1961). Modern populations were first established in 1963 in the Askania Nova biosphere reserve (Treus & Lobanov, 1974); these artificially formed semi-free groups existed in Askania until recently, and are now likely to have been destroyed by the occupiers. Such work allowed the Askania population to reach the level of 60–70 specimens, and in 2002 there were already 180 onager in Ukraine, and in another 20 years (as of 01.01.2022) the total number of onager in Ukraine increased to about 500 individuals (Yasynetska, 2022). Of this number, more than 173 individuals, or 34%, lived in the Askania Nova reserve (ibid.), and about 200–300 individuals lived in the Azov-Syvash NNP, on Byriuchyi Island (Polzyk, 2020), but the current situation there is unknown.

Despite these trends in the population of onager in Ukraine, the state statistics (2tp-hunting) did not include onager for a long time: the last time they were listed in the tables was in 2012 for Kherson Oblast (99 individuals) and in 2013 for Mykolaiv Oblast (20 individuals); in the subsequent 2014–2021, the tables of game fauna records showed 0 individuals of this species. This contradicts the actual data cited above, which can only be explained by the fact that populations from protected areas are not included in the '2tp' form assessments.

In addition to the data on onager in Askania-Nova reserve and Azov-Sivash NNP (Byriuchyi Island), a series of new releases of the species to new locations in southern Ukraine took place. This resulted in the establishment of new local populations in Crimea in the Charivna Gavan NNP (Tarkhankut) and in Odesa Oblast in the Tarutynskyi Steppe NNP. The formation of these populations was accompanied by extensive media coverage, with many reports (including on the platform www.ukrinform.ua). Moreover, the activity of public organisations under the slogans of rewilding has developed, which was especially loud in Tarutino (MM-NM: Rewilding Danube Delta). Whether such introductions are reintroductions will be shown in the future. At present, we can only say that modern local phytocoenoses were probably formed without the participation of onager.

These data show that this species is actually found only in protected areas, i.e. it is 100% protected. No other mammal species has received such protection, except for the Przewalski's horse, which received similar protection after the establishment of the Chornobyl Radiation and Ecological Biosphere Reserve in 2016. List of individual locations of the species in the last 20 years:

Northern oblasts. * Kyiv Oblast, no locality, group of animals for dispersal, without data about population, 2020-2021 (Yasynetska, 2022); * Zhytomyr Oblast, Research Agricultural Station, 50.287931, 28.712655, 11.05.2023 (SN-INat: Dasha_Sak016).

Southern oblasts. * Odesa Oblast, group of animals for dispersal, without data on location and number of individuals, 2020–2021 (Yasynetska, 2022); * Odesa Oblast, Tarutyne Raion, 46.280181, 29.424284, in semi-free state, n = 4, 23.04.24 (SN-INat: V. Kolomiichuk); * Kherson Oblast, Askania-Nova Biosphere Eeserve [46.465238, 33.981740], n = 173, in 2022. (Yasynetska, 2022); * Kherson Oblast, Byriuchyi Island, Azov-Syvash NNP [46.126340, 35.086464], n = 200–300 (Polzyk, 2020); * AR of Crimea, Tarkhankut Peninsula, Charivna Gavan NNP, 45.463819, 32.499352 (n = 2, photo), 28.04.21 (SN-INat: V. Luzanov).

9. *Cervus nippon* Temminck, 1838 (sika deer). Status – AS3b (+ AS1c → AS3b). A mammal species from the family Cervidae of the order Cerviformes (Artiodactyla auct.). The sika deer is an alien introduced species that is bred in many hunting grounds in Ukraine (Evtushevsky, 2009). It was brought to Ukraine from Primorsky Krai. The animals were first brought to Askania Nova Zoo in 1909. The work on the distribution of this species continued in different regions (central and western) during 1956–1986. The most favourable territories for breeding sika deer were most hunting grounds of the forest-steppe and steppe zones. The animals have also become established in the forest zone.

The animals are characterised by their attachment to their territory; when snow falls, they can approach people's homes, and individuals raised in enclosures can look for additional food resources on household farms. The most recent introductions took place in 2000–2001 on the territory of Dubrovytsia, Mlyniv and Sarny forestry enterprises in Rivne Oblast. The animals were brought from the Dnipro-Bug sovkhoz in Belarus. In 2002, 48 individuals were resettled from Dashiv and Khust forestry and game farms to Kharkiv Oblast, to the grounds of the LTD 'EFR' (Evtushevsky, 2012).

The data on the population of *Cervus nippon* demonstrate a continuous and rapid growth of populations, with minor fluctuations (Fig. 7a). In recent years, this has been facilitated by hunting restrictions, but the rate of increase is in marked contrast to the prolonged depression of the native species, *Cervus elaphus* (Zagorodniuk, 2022). These two processes appear to be intertwined, which may indicate either a competitive relationship between these species or excessive favouring (by hunting ground users) of the alien species over the native one.

The analysis of the abundance of *Cervus nippon* by regions of Ukraine (Fig. 7b) shows predominantly higher numbers in the forest-steppe zone of Ukraine and to a lesser extent in the northern regions, particularly Volyn Oblast. The species was not recorded in a number of regions that are part of the southern steppe, and more generally in the main part of the steppe zone. The species has low abundance in the mountainous areas, and is not recorded in Zakarpattia and Bukovna.

10. *Dama dama* (Linnaeus, 1758) (Fallow Deer). Status – AS3b (+ AS1c → AS3b). A mammal species from the family Cervidae of the order Cerviformes (Artiodactyla auct.). An alien species for the Ukrainian fauna, it has successfully adapted to semi-free keeping in steppe habitats, including Askania Nova Biosphere Reserve, Azov-Sivash NNP, Dzharylgach Island and Tavria Zoological Park. In a 1961 report on historical changes in the fauna of Ukraine, it was noted that 'the free-ranging fallow deer in Ukraine still lives in one hunting reserve' (Sokur, 1961: 76). The first attempts to settle 6 fallow deer in semi-free conditions of the State Residence 'Zalissia' occurred in 1959–1960, which were further supported by numerous imports. The population reached its highest numbers in 1998 (184 individuals), but in different periods the dynamics of the population has been subject to decreases and increases, for example, already in 2002 the number in Zalissia was 66 individuals (Smagol et al., 2005), and as of 2012 the number of the species there was 120 individuals (Evtushevsky, 2012).

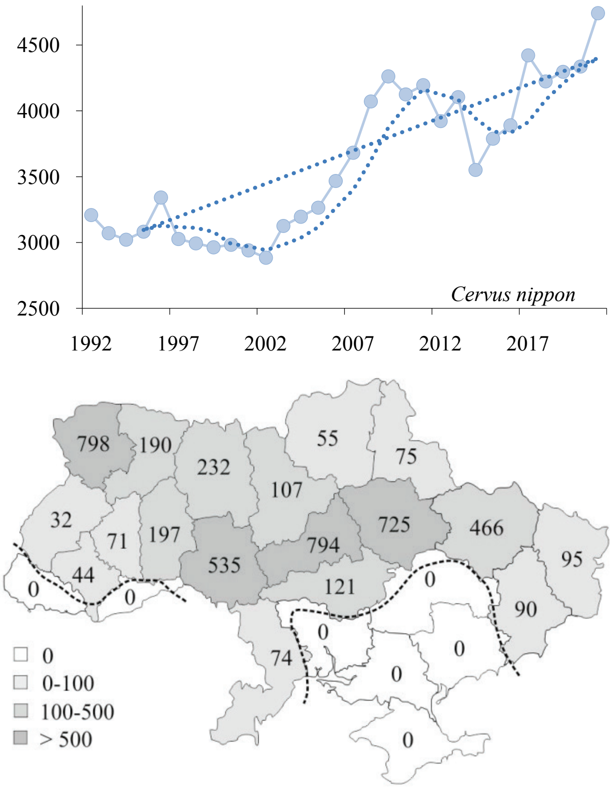

Fig. 7. *Cervus nippon* in Ukraine according to hunting statistics for the period from 1992 to 2021: long-term population dynamics (*a*) and distribution of data by regions as of 2021 (*b*); the line indicates regions where the species is absent

At the beginning of the 21th century, on the territory of Ukraine there were small areas with fallow deer in Dnipropetrovsk, Odesa, Mykolaiv, Zaporizhzhia and Kherson oblasts, where the main population existed in the Azov-Syvash NNP, Byriuchyi Island (Volokh, 2014). The total numbers of the species in Ukraine, according to statistics on 2tp hunting, was 3.2 thousand individuals as of 2012. As of 2020, there were 1397 individuals in Ukraine (according to the 2-tp), but this estimate was preceded by a 'collapse' in numbers in 2011–2012 (Fig. 8a). The distribution across Ukraine is uneven, the species is almost absent in the steppe regions, more common in the forest-steppe (Fig. 8b); the 'spot' of high numbers in the south (Kherson Oblast) is primarily due to the formation of an artificial population on Dzharylgach Island, which began in 1989, and where the optimal number is currently exceeded by 1.9 times. The number of these animals on the island, as of 2003, was 110 individuals, in 2015 – up to 200 individuals, in 2021 – 154 individuals (Sheihas, 2023).

There are many reports of fallow deer sightings, which is understandable given the total population of over 3,000 individuals. However, a significant proportion of the population lives in enclosures and island type hunting grounds, i.e. outside the free range of the species. Nevertheless, escapes occur regularly, and the species is often spotted in the vicinity of various settlements, but is often mistaken for roe deer (despite its light colour and other characteristics). This is a feature of Ukrainian populations, as in many countries fallow deer are called 'park animals' and are encouraged to settle in suburban and other green areas. Examples of actual registrations in Ukraine over the past decade:

Northern oblasts. * Zhytomyr Oblast, (without location data), n = 6, 10.01.2024, in forest, in a felled area, probably escapes from an enclosure (SN and MM-YT, identified R. Romaniuk); * Kyiv Oblast, Boryspil Raion, n = 1, 06.09.2024, on the shore of a reservoir, without details (SN-FB: L. Tonkonoh); * Kyiv Oblast, Pushcha-Vodytsia forestry [50.537032, 30.417046], n = 6, 25.12.2016, one male and five females (SN-FB: Y. Rudenko); * Kyiv Oblast, Zalissia residency [50.894631, 30.871699], n = 1, 24.12.2017, (SN-FB: T. Tureiska), 50.682670, 30.864035; * Chernihiv Oblast, Nature Park Beremytske, n = 4, 24.04.2020; 14, 28.01.2022 (SN-FB: A. Zenchenko); * Kherson Oblast, Dzharylhach Island [46.029831, 32.889724], n = 1, albino, 27.08.2020, (SN-FB: M. Rudik); * Chernihiv Oblast, Mezyn NNP, Desna River [51.737304, 33.099780], n = 1, male, 5.08.2023, (SN-FB: K. Vityak-Radina); * Chernihiv Oblast, Nature Park Beremytske [50.894631, 30.871699], n = 2, 1.12.2023, (SN-FB: D. Bozhenok); * Poltava Oblast, agricultural land (field), n = 1, 02.06.2023, without details and location information (SN-FB: Z. Srybnaia); * Cherkasy Oblast, Melnyky, 49.160234, 32.276906, n = 1, 18.05.2024, (SN-INat: K. Lavrinenko); * Chernihiv Oblast, Kozelets Raion, Ostrokhy, n = 6, appeared in winter 2023–2024, escape from a private HG 'Maksym', at night and at dusk, they often go to vegetable gardens and visit abandoned yards, eating fallen apples (PC-B: A. Sahaidak).

Podillia. * Vinnytsia Oblast, Haisyn Raion, 48.758595, 29.111533, n = 1, 2.03.2015, (SN-UkrBIN: O. Zhmurko).

Carpathian Mountains. * Female with fawns, n ≈ 11, 14.01.2022, without details and data on the exact location (SN-FB: P. Kondrat).

Southern oblasts. * Kherson Oblast, Henichesk Raion, Byriuchyi Island, 46.118973, 35.049791, n = 1, 22.10.2020 (SN-INat: N. Suriadna); * Kherson Oblast, Oleshky Sands, 46.629463, 32.944725, n = 1, 22.07.2020 (SN-INat: katushka_grushka); * Kherson Oblast, Dzharylhach [46.026230, 32.890835], fallow deer on the island since 1989 (Sheihas, 2023).

In general, actual records of the species confirmed its presence in Kyiv, Zhytomyr, Kherson, and Zakarpattia oblasts, but it was also recorded as an alien species in Chernihiv Oblast, as evidenced by repeated records of the species in Beremytske Nature Park and Mezyn NNP, which was not reflected in the statistical reporting as of 2021.

11. *Ovis gmelini* Blyth, 1841 (mouflon). Status – AS3b (AS3b → AS3c). A mammal species from the family Bovidae of the order Cerviformes (Artiodactyla auct.). Animals of this species were first brought to Ukraine to Askania Nova in 1894; they were also brought to Askania after the Second World War, from Italy and Czechoslovakia (Evtushevsky, 2012). Mouflons were also brought to the mountainous regions of Crimea (10 purebred animals and three hybrids with domestic sheep: Dulitsky & Kormilitsyn, 1970). For a long time, this Crimean population was essentially the only free-living population in Ukraine (Dulitsky, 2010); its fate is currently unknown. An artificially isolated population was also formed in the Zalissia Residence, which was maintained by importing large batches of new animals, but since the mid-1990s, mouflon have not been found there (Evtushevsky, 2012).

In 1976, 10 mouflon were brought to the Azov-Sivash NNP, which bred and within 15 years formed a population on Byriuchyi Island with a population of about 1000 individuals. In March 1998, there was a sharp decline in the population on Byriuchyi Island when the low-lying part of the peninsula was flooded. A strong island-type population of mouflon was formed on Dzharylgach Island after the species was introduced there in 1993. This population accounts for the largest share in the overall population dynamics and, accordingly, the graph clearly shows a decline in their numbers between the late 1990s and early 2000s. In particular, at the beginning of 2022, 314 individuals lived on the island, exceeding the optimal number by 4.1 times (Sheihas, 2023).

According to media reports, under the occupation, the entire game fauna of Dzharylgach, as well as Byriuchyi Island, was destroyed by the Russian occupiers. Information about mouflon sightings available in open sources (SN) is related to these territories. For finds in other regions with statistical information, the results of which are shown in Figure 9a-b. It is likely that the presence of animals in certain regions is related to their semi-free keeping in isolated areas.

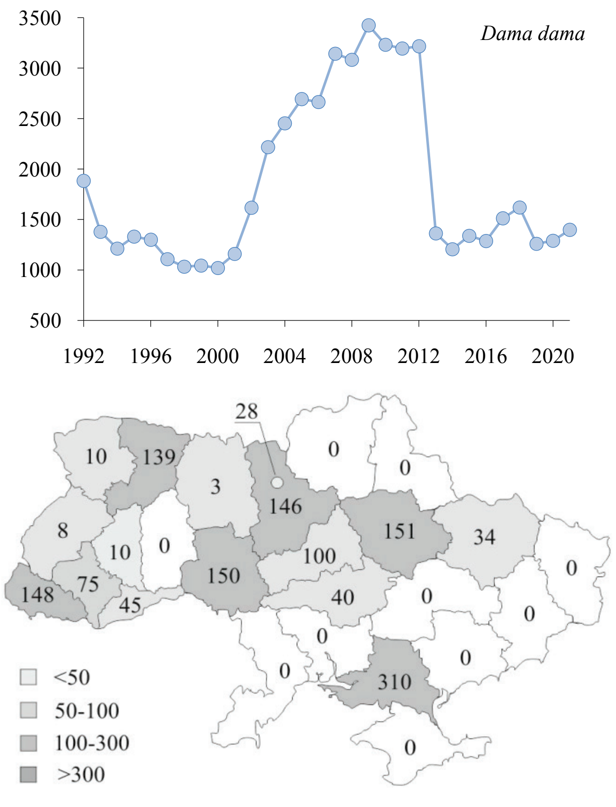

Fig. 8. *Dama dama* in Ukraine according to hunting statistics for the period from 1992 to 2021: long-term population dynamics (*a*) and distribution of data by oblast as of 2021 (*b*)

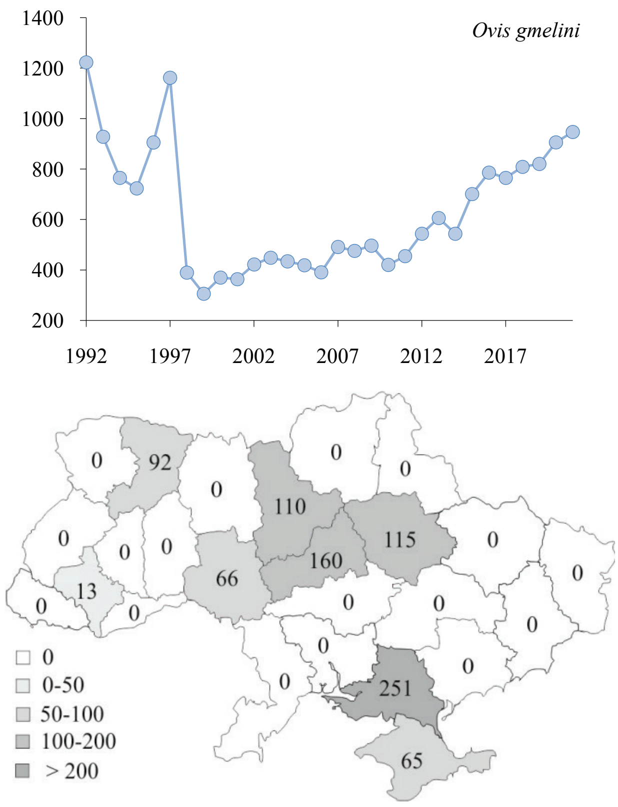

Fig. 9. *Ovis gmelini* on the territory of Ukraine according to hunting statistics for the period from 1992 to 2021: long-term population dynamics (*a*) and distribution of data by oblasts as of 2021 (*b*)

Guild structure

The entry of new species into native (new to them) biotas is limited by various biotic factors, not only abiotic ones. Often, such an introduction is limited by the extremely high density (packing) of biotic communities, which in animals is most clearly manifested at the level of guilds. Most often, guilds of consumers are organised into linear groups, in which individual elements (species) are distributed according to metric features correlated with the size of victims, i.e. available food. This pattern is found in different groups, and is especially evident in vertebrates.

It is well known that species in communities (and, in fact, in guilds) are often distributed by their characters important for foraging along the gradient of forage resources in a non-random way, with a step close to the Hutchinson constant (Hutchinson, 1959), i.e. 1.26 for metric characters or 2.00 for weight characters (1.26 = cube root of 2). This phenomenon has been the subject of many studies, both on the niche concept (e.g., Petren, 2001) and on the regularities of such distribution (Dayan & Simberloff, 2005; Pfennig & Pfennig, 2009; Stuart & Losos, 2013). The application of this regularity to the analysis of the structure of the Ukrainian mammal fauna was presented in one of our previous reviews (Zagorodniuk, 2008), and even earlier it was successfully tested on the guild of ungulates (Vyshnevskyi, 2002), and later on mustelids (Zagorodniuk, 2009) and bats (Zagorodniuk, 2018). The 2008 paper presents models that contain 'vacancies' ('windows') or include introduced species.

The guild structure was studied using the analysis of a number of morphometric traits related to foraging. These characters can be the overall size of the body, skull, or dental system. We used the length of the skull as the most accessible parameter. The sources were data from the authors' previous publications (not all of which are cited here due to self-citation restrictions) and numerous publications by colleagues. In all cases, we are talking about the condylobasal length of the skull. All relevant references are listed in Table 4.

The guilds are named after their typical species, and such names do not always reflect the details of the taxonomy (e.g., species composition of families), although they are close to it. In some cases, guilds are formed by species of different families. The names of the guilds are followed by their interpretation, which is not exhaustive, but characterises the common features of the species in their composition. In total, six guilds are considered that include introduced species (in one case there is also an invasive species: position 3.3 in Table 4). Rank positions within the four size classes considered here are presented for all species, although it is clear that there could be more ranks (e.g., in the mustelid guild, the lowest rank would be '0' for *Mustela nivalis*). The names of introduced, reintroduced, and invasive species are given in bold.

Table 4
Guilds with inclusions of alien introduced species:
only four guild ranks are shown, which are related to the positions of alien species; names of the alien species are in bold*

Guild	Rank 1 (small-sized)	Rank 2 (lesser)	Rank 3 (great)	Rank 4 (greater)
1. Leporid guild (species of phyto/coprophages)	Steppe pika (†) *Ochotona pusilla* 33–39 [1.1]	**European rabbit** *Oryctolagus cuniculus* 65–68 [1.2]	Mountain hare *Lepus timidus* 83–95 [1.3]	European hare *Lepus europaeus* 96–104 [1.4]
2. Arvicolid guild (semi-aquatic phytophage rodents)	European water vole *Arvicola amphibius* 36–43 [2.1]	**Muskrat** *Ondatra zibethicus* 55–67 [2.2]	**Coypu** *Myocastor coypus* 94–117 [2.3]	Eurasian beaver *Castor fiber* 115–148 [2.4]
3. Canid guild (large carnivores from family Canidae)	**Raccoon dog** *Nyctereutes procyonoides* 105–130 [3.1]	Red fox *Vulpes vulpes* 137–166 [3.2]	**Golden jackal** *Canis aureus* 171–181 [3.3]	Wolf *Canis lupus* 195–250 [3.4]
4. Mustelid guild (semi-aquatic carnivores)	Stoat *Mustela erminea* 44–53 [4.1]	**European polecat** *Mustela putorius* 53–68 [4.2]	European mink *Mustela lutreola* 56–66 [4.3]	**American mink** *Neogale vison* 58–72 [4.4]
5. Equid guild (large steppe phytophages)	**Saiga antelope** (†, reintr.) *Saiga tatarica* 240–253 [5.1]	**African wild ass** (†) *Equus africanus* 390–490 [5.2]	**Onager** (†, reintr.) *Equus hemionus* 504–544 [5.3]	**Wild horse** (†, reintr.) *Equus ferus* 529–615 [5.4]
6. Cervid guild (large forest phytophages)	Roe deer *Capreolus capreolus* 184–205 [6.1]	**European fallow deer** *Dama dama* 231–283 [6.2]	**Sika deer** *Cervus nippon* 270–331 [6.3]	Red deer *Cervus elaphus* 396–432 [6.4]

Notes: * numbers in square brackets indicate references to sources (both original data and data from the literature are presented), including: [1.1] – Wilson et al. (2016); [1.2] – Falzon (2019); [1.3] – Angerbjörn & Flux (1995); [1.4] – Bock (2020); [2.1] – data of the authors; [2.2] – Lazariev (2023b); [2.3] – Woods et al. (1992); [2.4] – Nowicki et al. (2019); [3.1] – data of the authors; [3.2] – Csányi et al. (2023); [3.3] – Markov et al. (2017); [3.4] – Lebedeva et al. (2017); [4.1]–[4.3] – Zagorodniuk (2009); [4.4] – Lazariev (2024); [5.1] – Stekleniov & Smagol (2013); [5.2] – Zhu et al. (2014); [5.3] – Groves (2002); [5.4] – Merkies et al. (2020); [6.1] – data of the authors; [6.2] – Feldhamer et al. (1988); [6.3] – Smagol & Smagol (2020); [6.4] – Kravchenko (1971).

The results fully confirmed our initial assumptions. It is obvious that the success of introductions is determined by the presence of free niches, or niche 'gaps', in the structure of guilds. If such gaps are absent or too narrow, then the introductions will either be unsuccessful or lead to the extinction of the natives. Obviously, for successful introductions, species niches (in our case, in the eco-morphological dimension) should not only not overlap, but also not collide. At the same time, such concepts of ecomorphological niches cannot be considered as a static system. It is dynamic in both space and time. In particular, species can be allopatric or characterised by only marginal sympatry, as we have described for a number of groups of ecomorphologically similar native species (Zagorodniuk, 2018, 2019).

As can be seen from the data presented in the table, introduced species (and partly invasive species from the same guilds) in most cases find themselves in significant niche 'vacancies', where the term 'vacancy' is equivalent to the term 'free ecological niche' (sensu Levchenko & Starobogatov, 1990). In the context of this study, such 'vacancies' can be referred to as 'windows in the guild structure'. Introductions of semi-aquatic species are particularly successful, due to the high ecological capacity of floodplain complexes (including their eutrophicity) and the wide 'windows' in the structure of ecomorphological differentiation of guilds. In general, all guilds are harmonised, and all alien species have integrated into them without any problems, entering the appropriate 'windows'. Moreover, in many cases, adjacent positions are 'occupied' by either de facto extinct species or rare and threatened species, with which de facto aliens may not overlap.

In addition to eutrophicity, the effectiveness of introductions of amphibious mammals is determined by two other features of such ecosystems, namely virginity (relatively low disturbance) and continuity (ecocorridor status). Together, these three features determine the ability of species to disperse smoothly and rapidly along river basins and their respective landscape catenae. The same features are also important for the distribution of many aboriginal and invasive species, so they are universal. These features have been repeatedly highlighted in our previous works, both in relation to the mammalian fauna as a whole (Zagorodniuk, 2006) and in the analysis of river systems as corridors of expansion (Lazariev, 2023a). Similar expansions have also occurred in the more distant past (Popova et al., 2021).

A brief description of the six guilds identified here, including introductions, is as follows.

1. Leporid guild. One of the least remarkable guilds due to the lack of all but one of the above-mentioned species in the region of our attention:

the European hare (*Lepus europaeus*). The guild is four-membered, but one of the species is extinct in Ukraine (*Ochotona pussila*) and another has an extremely marginal distribution (in the north, *Lepus timidus*). At various times, there have been attempts or only ideas to reintroduce both of these species in different regions, including *Lepus timidus* in the Carpathians and *Ochotona pussila* in the Dnister Canyon. In the end, these reintroductions failed, but another species, the European wild rabbit (*Oryctolagus cuniculus*), was successfully introduced in dozens of locations. This species, new to the local fauna, fits very organically into the size range of the guild (see Table 4), without overlap with neighbouring species. The issue of similarity and convergence of characters in the process of rabbit acclimatisation was considered by Volyansky (1924). Calculations based on his data showed a high level of differences in external traits at the level of Hutchinson's ratio HR = 1.49–1.85 (Zagorodniuk, 2023a). Also, B. Volianskyi noted that wild rabbits from near Odesa had clearly grown larger over time and approached hares in size and proportions. Nevertheless, the populations of this species in Ukraine, once very numerous, have declined due to zoonoses (Zagorodniuk, 2023a), as well as the fact that this species was extremely conservative in terms of locations, with weak dispersal abilities, which occurred only within the tracts in which it was introduced (e.g., Vikyrchak & Bachynskyi, 2019). Thus, this guild turned out to be the least complete, with no prospects for development at the level of regional faunas.

2. Arvicolid guild. One of the most successful guilds among those considered here, defined by both phytophagy (i.e., an unlimited resource) and a wide range of size differences between species and a distinct connection with river basins, especially plains, and the ability to live in both natural and artificial water bodies. The structure of this guild was described earlier (Zagorodniuk, 2008). In fact, it contained only two very different-sized natives from different families (*Arvicola amphibius* and *Castor fiber*), between which there was a significant ecomorphological 'window'. That is why muskrat (*Ondatra zibethicus*) and coypu (*Myocastor coypus*) have been perfectly integrated into this guild as aquatic phytophages. Muskrats are much larger than water voles (Lazariev, 2023b), even taking into account age-related variability, which allows them to be more adaptable and competitive, especially against the background of the decline in *Arvicola amphibius*. However, both we (see Fig. 2) and our colleagues from Poland (Dziech et al., 2023), where the 'natural' migration of animals to Ukraine (with new introductions) took place, have observed a steady decline in muskrat numbers in different parts of the range over the past 15 years. A possible reason for this may be zoonosis (previously, *Arvicola* was the main reservoir of tularemia). The second species, coypu, having a good 'window' in the guild structure, was trapped not by biocoenotic but by climatic factors, and only global warming became a trigger for the development of spontaneous introduction, based on the escape of animals from captivity. Coypu does not pose a threat to muskrats due to their low adaptability to the natural conditions of Ukraine, and there is a large ecomorphological distance between them (Zagorodniuk, 2008), which is also an important phenomenon when the 'window' allows two alien species, *Ondatra zibethicus* and *Myocastor coypus*, to coexist normally.

3. Canid guild. The guild, the components of which are the objects of special attention from many specialists, game experts, and conservationists; these are species of the family Canidae. The two native species were joined by one introduced species (*Nyctereutes procyonoides*) and one alien species (*Canis aureus*), which was introduced conditionally by natural means, against the background of three factors: the decline in wolf numbers, global warming and a number of wars in the south. Both of these species (raccoon and jackal) fit very well into the structure of the local carnivore guild, occupying their respective ecomorphological niches without any overlap with the natives (Table 4). Their order, unlike other guilds, is alternating, alien < native < alien < native (raccoon dog < fox < jackal < wolf). Moreover, there is a 'window' between the first two species for another very rare native, the steppe fox (*Vulpes corsac*). Since there is no actual overlap with *Vulpes corsac* (the steppe fox is found only in the eastern steppes, and the raccoon tends to floodplains), this introduced species feels quite comfortable, occupying an essentially marginal position in a guild where there is no two-way pressure from adjacent species (Table 4). The widespread recent expansion of the jackal and its entry into the local canid guild can be explained by the fact that it has virtually no competition with the fox and at the same time does not feel pressure from the wolf, especially in the south and in floodplains (Rozhenko, 2017), where the wolf is essentially absent or extremely scarce. Furthermore, the jackal may be a species that has been extinct for some time and has now returned to its 'window' (Zagorodniuk, 2014).

4. Mustelid guild. In the scope of the Ukrainian fauna, the guild includes 7 species of *Mustela* s. l. (together with '*Mustela*' *vison*). Its structure has been described previously, including an analysis of size differentiation by sex, the contribution of age-related variability and the level of sympatry (Zagorodniuk, 2009). In fact, there is only one introduced species in this guild, the American mink, which has relatively easily joined this guild (Zagorodniuk, 2009). According to the authors' hypothesis, its entry was preceded by the expansion of the European polecat (*Mustela putorius*) from the north and the steppe polecat (*M. eversmanni*) from the east. The latter species in the context of the 'floodplain' part of the guild, is exclusively terrestrial (steppe) and therefore excluded from the analysis, as well as the species *Vormela peregusna*. In fact, the appearance of *M. eversmanni* significantly narrowed the available 'windows' in the guild (see Table 4), but the plasticity of this species allowed it, as is typical for many alien species, to occupy synanthropic habitats, although it is rare in them. The key factor for the existence of a stable guild structure was eventually the appearance of *Neogale vison*, which quickly populated the entire network of artificial reservoirs (reservoirs, fish farm ponds and simple ponds). Its appearance actually meant a conflict with the native mink and its extinction (Panov, 2002). Only in those places where the American mink is absent does the native mink maintain relatively stable populations, such as the Lower Dnister (Rozhenko, 2015). The same processes are taking place in all other regions of Europe, where the appearance of the American mink quite predictably led to the extinction of populations of the native species (Põdra & Gómez, 2018).

5. Equid guild. Size differentiation between equids is significant (Nacarino-Meneses, 2023), and this guild is one of the most obvious (Vyshnevskyi, 2002), but at the same time the most destroyed, incomplete: large mammals from large open spaces disappeared along with the disappearance of the steppe as a zonal ecosystem. This happened for many reasons, including the ploughing of the steppe and the direct extermination of these animals, and not only and not so much for food, but also for a number of other reasons (the persecution of wild horses, whose stallions led domestic mares into the steppe, is well known). As a result, most species of this guild have disappeared over the past three centuries, although not simultaneously, but alternately (Sokur, 1961). In addition to the *Equus* species (s. l.), we also include the saiga (*Saiga tatarica*) from the family Bovidae (Table 4). In fact, all species are objects of various reintroductions, some of which are quite successful, but all of them are limited in space: in fact, all of them are in isolated territories of protected areas, such as the Chapelsky Pod section of the Askania-Nova Biosphere Reserve, Byriuchy Island as part of the Azov-Syvasky National Park, Dzharylgach Island as a territory belonging to the national park of the same name, the Chernobyl Exclusion Zone, which is now the Chernobyl Biosphere Reserve, etc. (Yasynetska, 2022; Sheihas, 2023). That is, all such populations are not only isolated, but also exist under conditions of protection and important biotechnical measures: watering holes, salt pans, feeding, predation limitation, poaching control. In fact, reintroductions in limited spaces may not be consistent with either the guild structure or even the genetics of the reintroduced species: the main thing here is the restoration of certain ecosystem functions that domestic forms can perform, as was implemented in the Khomutovsky Steppe reserve, where domestic horses were kept on free grazing for many years (Tkachenko et al., 2009).

6. Cervid guild. One of the most notable guilds with a distinct size range. The presence of three native species of the group 'roe deer < red deer < elk' (*Capreolus*, *Cervus*, *Alces*) is one of the best illustrations for demonstrating the principle of limiting similarity and Hutchinson's ratios (Zagorodniuk, 2008). Moreover, in this guild there is a distinct 'window' on the 'roe deer–red deer' segment, which is partially occupied by the wild boar (*Sus scrofa*). Both introductions very neatly filled this 'window': the fallow deer (*Dama dama*) and the sika deer (*Cervus nippon*) organically occupied it. The success of such introductions has been noted by colleagues (Evtushevsky, 2009; Sheihas, 2023), which is determined by their cer-

tain harmony with the structure of this guild (Table 4). Moreover, within all these species there is a pronounced sexual dimorphism, which 'slides' the sexes into separate ecomorphological subniches. Thus, according to data from available sources, females and males of *Cervus nippon* do not overlap in cranial characters: the skull length in females is 270–298 mm, and in males is 301–331 mm (Smagol & Smagol, 2020). Given that large mammals are confined to small refugia and do not form large overlapping geographical ranges, any conflicts between them are limited or even impossible. In particular, these are conflicts that could arise due to the overlapping ecomorphological profiles of different age groups of related species (e.g., old male of roe deer vs young female of fallow deer). Instead, the realities are such that the species of this guild are distributed in a very mosaic manner, often in a 'checkerboard' pattern, with the formation of incomplete local guilds, 2–3 species in each location.

Discussion

First, it should be noted that the sources of information about introduced alien species are very diverse in terms of the number of reports. In particular, amateur projects such as GBIF and INaturalist (in contrast to UkrBIN and DC-BDU) gave us a significant share of information about introduced species, which indicates both the strengthening of the position of citizen science and other features of this data: a) such sources contain a large array of data on finds of alien species, collected by amateurs, which indicates the significant distribution and abundance of these animals; b) most species records, and therefore their ecological specificity, are often associated with disturbed habitats. As result, most reports of finds are related to human settlements, in particular areas of large urban agglomerations. This concentration of finds is also due to the fact that amateur observers usually do not go far from populated areas to observe nature.

This variety in data quality is very similar to the described problem of information completeness and access to it in non-English scientific sources (Angulo et al., 2021): it is noted that an important source of data on invasive species is hard-to-reach literature (including 'grey' literature and regional publications), unpublished faunal report data, particularly in linguistically diverse sources, including those outside the English literature: non-English sources collect comparatively more data. And this is an important factor in supporting our applied search for data from various sources, including amateur communities and networks such as INaturalist or Facebook.

Here it is important to consider the following five issues: 1) taxonomic diversity and biotopes of introduced species, 2) measures to regulate the abundance of introduced species, in particular through regulated hunting on them, 4) effects of hostilities, in particular the formation of an overdeveloped belligerative landscape, 5) climate change as a contributing factor to populations of introduced species. These components are an important regional addition to the list of drivers of biological invasions (transportation, climate change, and socio-economic change), consideration or management of which can reduce the negative impacts of alien species (Essl et al., 2020). Obviously, the scenarios for invasive species may be different from those of introduced ones, particularly with respect to transport and targeted or unintentional species support programmes. The specifics of introduced species, in particular, in the conditions of their existence in Ukraine, are considered further according to these five components.

It is important to point out that not all introductions were successful. For example, before the Second World War (1936–1937), striped skunks (*Mephitis mephitis*) were introduced in Kharkiv Oblast, but after the war, no traces of their presence were found (Kolosov & Lavrov, 1968). In the postwar years, 10 species of mammals (mostly ungulates) were introduced within the Crimean Game Reserve alone (Dulitsky & Kormilitsyna, 1975), but only one of them, the mouflon, survived (Dulitsky, 2010). The European rabbit (*Oryctolagus cuniculus*), which was successfully introduced at the beginning, also suffered extinction, both at the level of separate local populations (Vikyrchak & Bachynskyi, 2019) and in Ukraine as a whole (Zagorodniuk, 2023a). A factor of their vulnerability was that all known rabbit settlements remained locally restricted, without any noticeable expansion of the species beyond the tracts in which it was introduced, in addition to the development of zoonoses that finally eliminated them (ibid.).

There were also a series of other introductions, such as the introduction of pigs from the Far East to the Crimea, Siberian red squirrels in the Crimea and Donets, mountain hare (*Lepus timidus*) in the Carpathians, etc. (Sokur, 1961). However, such introductions concerned either subspecies or species already known in the fauna of Ukraine in other regions. The introduction of a number of ungulates, such as kulan (Equus *hemionus*), is exclusively local. Only in a semi-free state and in sporadic occurrences do the Indian buffalo (*Bubalus bubalis*) and a number of other species (Bactrian camel, donkey, eland, etc.) exist in Ukraine (Treus, 1974; Zagorodniuk, 2023b).

Normally, all alien species are typical synanthropes or inhabitants of disturbed habitats and ecosystems. This thesis is absolute and universally recognised, as has been stated many times (e.g. Parker et al., 1999; Zagorodniuk, 2006). In particular, the inhabitants of agrocoenoses (primarily fallow land and ruderal coenoses) demonstrate wide expansions, which in ancient times were demonstrated by ground squirrels (Spermophilus), steppe lemmings (*Lagurus lagurus*) and common voles (*Microtus* ex gr. *arvalis*). In the modern period of fauna development, active dispersal is demonstrated by the mound-building mouse, *Mus spicilegus*, which has significantly moved northwards over the past 2–3 decades (Zagorodniuk, 2019; Vikyrchak, 2020). However, there are virtually no successful introductions among the inhabitants of agrocoenoses, either as a result of targeted introductions (under land improvement programmes and/or to limit pest populations) or escapes from captivity. Similarly, there are no successful introductions in steppe communities, and in forest regions (Polissia and the Carpathians), the faunal change index is one of the lowest in general, with no more than 3–5% change in species composition for over 100 years (Zagorodniuk, 2010). In fact, this is the answer: introductions form the most successful populations in three types of habitats: forest-steppe, marginal habitats, and intrazonal complexes.

The expansion of alien mammalian species largely depends on the connectivity, or, conversely, on the isolation of habitats, which in turn depends on the landscape character (Coulon et al., 2004; Cushman et al., 2006). In this regard, waterways play a significant role, as they are important routes for the expansion of invasive species (Fischer, 2017). It is important to note two other habitat-related features of invasive species, especially in view of the current conditions in Ukraine. Alien species inhabit not only disturbed and synanthropic habitats, but also floodplain ecosystems of river networks. River floodplains are characterised by a high level of eutrophication (a larger food base and dense guild packing) (MacArthur, 1970; Rappoldt & Hogeweg, 1980).

While in the first types of habitats species are established due to the lack of competition and increased predation pressure, in floodplain ecosystems this success is ensured by high food supply, concentration of microhabitats, and higher ecosystem productivity. Despite the high productivity of floodplains, they are characterised by a high degree of naturalness and determine the success of alien species in floodplain complexes due to three factors: eutrophicity, naturalness, and continuity. Those introductions that are successful in floodplains are exanthropes (Zagorodniuk, 2006). Their success in floodplain complexes is not accidental and is due to these three features, including the relative ease of integration into the structure of guilds. While in disturbed ecosystems, which are recognised as the main springboards for invasions, a favourable factor is reduced competition and predation, in floodplain and generally in riverine complexes, this factor is a high concentration of resources. These are eutrophic coenoses, which are the easiest to integrate into. This is best demonstrated by large-sized rodents and carnivores of various sizes.

The same habitats are also favourable for those alien species that have become naturally introduced and demonstrate wide expansions, such as the golden jackal, *Canis aureus* (Rusev, 2020; Rozhenko, 2021; Zhyla, 2023). In fact, the vison ('American mink') also appeared in Ukraine not as an introduced species (it was later that numerous escapes from captivity took place), but as an invader in the Dnipro basin from Belarus (Panov, 2002; Zagorodniuk, 2023b). Almost all of these species, except for ungulates, correspond to these ecological characteristics, but ungulates are also dependent on water resources (watering holes), which is fully true for Ukraine, both in the southern coastal areas (Polzyk, 2020) and Polissia (Zhyla, 2022).

The behaviour of introduced species in the places of their introduction is very different. The system for classifying and analysing the degree of adventitiousness is detailed by botanists who classify alien species according to three criteria: time of appearance (archaeophytes, kenophytes, neophytes), mode of appearance (xenophytes, ergasiophytes) and degree of naturalisation (agriophytes, epecophytes, colonophytes, ephemerophytes, ergasiophygophytes) (Richardson et al., 2000; Kucher, 2014). This classification is broader than the three-tiered system we proposed (Zagorodniuk, 2023b), and its first two components do not actually apply to mammal introductions; however, it is important for describing the extent of introductions in terms of naturalisation. Such degrees of naturalisation are determined by the ability of a species to form fully exanthrope populations and expand its range to cover new areas. The existing and described above variants of naturalisation levels can be divided into 5 groups (models). This does not include cases of unsuccessful introductions that resulted in extinction.

Model 1: locally restricted introductions with support, but without dispersal (botanical equivalent – ephemerophytes and colonophytes). In fact, these are the cases that had or have temporary success and are completely dependent on all care options, i.e. biotechniques (feeding, creation of shelters) and direct care (guarding, settlement of 'fresh blood'), etc. We have such situations with kulans (*Equus hemionus*) and partly with coypu (*Myocastor coypus*), which actually do not go beyond the places of introduction and are largely or completely dependent on people. The same model includes the northern raccoon (*Procyon lotor*), which sometimes appears in different places (a number of cases in the east and north of the country) and in the urban environment is quite dependent on human settlements.

Model 2: locally restricted introductions without special support, but also without dispersals (botanical equivalent – colonophytes). This model covers cases when, as a result of introduction, only local (island-type) foci of existence of the species were formed, without the formation of settlement zones outside the tracts. An example of this was the introduction of the European rabbit (*Oryctolagus cuniculus*). The animals occurred near the places of initial introduction, or settled locally at short distances.

Model 3: introductions followed by local self-dispersal (botanical equivalent – epecophytes). Despite the possibility of migrations, animals do not form a continuous wide range and have island-type settlements (colonies). This model includes the wild horse (*Equus ferus)*, a local population with facts of self-distribution has already formed in the Central Polissia. The same pattern was shown by other ungulates, in particular mouflons (*Ovis gmelini*) and fallow deer (*Dama dama*).

Model 4: introductions and subsequent independent wide-range dispersal (botanical equivalent – agriophytes). A clear example of this model was the independent expansion of the muskrat (*Ondatra zibethicus*), which is characterised by a wide and rapid expansion throughout the territory of Ukraine, even in the southern steppe regions along the networks of artificial watercourses (Selyunina et al., 2019), as well as the American mink (*Neogale vison*) and raccoon dog (*Nyctereutes procyonoides*). The same pattern is demonstrated by ungulates, in particular the sika deer (*Cervus nippon*).

Model 5 (mixed): Invasion from abroad followed by extensive expansion. Against the background of wide dispersal from remote places of introduction, 'local' introductions are also characteristic, in the form of escapes from captivity (category AS3c with secondary numerous AS1c). A similar type is shown by the vison ('American mink'), which as a result of expansion from Belarus in the 1960s appeared in the upper reaches of the Kyiv Reservoir, and along with this, a number of introductions took place in different regions of Ukraine (Panov, 2002). The muskrat also appeared and spread widely in several ways; there were both introductions (in most regions) and expansion from the territory of Poland, in Lviv Oblast (Tatarynov, 1952). Both introductions and parallel expansions have been recorded in relation to the raccoon: a number of introductions given in the text and recent facts of the raccoon occupying new territories within the borders of Polissia (registration of the species in Nalibotska Pushcha, in Belarus, detection of the animal in the territory of the checkpoint 'Mykolaivka' in Chernihiv Oblast).

The factors contributing to the appearance and distribution of introduced species were the following five:

1) keeping in captivity with the possibility to escape (in peacetime), as in the case of the dispersal of the American mink (Panov, 2002), which significantly expanded its range in places where special resettlement measures for this species were not carried out, in particular in the eastern regions of Ukraine (Lazariev, 2023a). Escapes from captivity are often registered in places where coypu breeding farms were established, as evidenced by the information on a number of finds of these animals given in the text;

2) the abandonment and destruction of various types of farms in which such species were kept (in conditions of hostilities), which caused the escape into nature of various animal species, in particular domestic ones, i.e. also foreign species, as well as the forced relocation of aboriginal species to atypical biotopes. As a result of military operations, it is expected that the list of alien species will increase and the populations of stenobionts from the aboriginal fauna will decrease (Zagorodniuk, 2024), which in turn opens up additional opportunities for the naturalisation of invasive animal species in new territories;

3) a decrease in the levels of presence, role and influence of native species, often observed along with the increase in abundance and expansions of ecologically close alien species: the reduction of the participation of a certain native species in the local fauna frees up space for the entry into the guild of a species new to this local fauna. A particularly noticeable effect on the decrease in the abundance and distribution of local species is caused by the appearance of alien predatory mammals (Zagorodniuk, 2006);

4) the increase in the share of disturbed (transformed) biotopes significantly contributes to the suppression of the state of populations of representatives of aboriginal fauna as a result of not only the direct destruction of habitats, but also the increased role of alien species in conditions of low (or no) competition with ecologically close native species, which could prevent the spread of new species of animals;

5) reduction of anthropogenic pressure and all forms of management and regulation of the presence of certain species. As a result of the decrease in the level of agricultural activity, there is a decrease in the presence of a number of stenobiont aboriginal species, in particular in the steppes (Lazariev et al., 2020). This creates additional conditions for increasing the abundance of alien species. The volume of bagging of alien animals does not correspond to the tasks of their eradication, and in the case of species that have distributed significantly and reached high abundance (*Ondatra zibethicus*), the implementation of such measures is unrealistic.

It is well known that in all situations studied in detail, the impacts of alien species, especially introduced ones (that have not naturally penetrated as a result of range expansion) on the native biota are negative. This is evidenced by many special studies, but it is also clear from the viewpoint of general knowledge about the structure of faunal assemblages (Parker et al., 1999; Mooney & Cleland, 2001; Sanders et al., 2003), including the mammal fauna of Ukraine (Zagorodniuk, 2006). The negative impact of alien introduced species is also known from a number of publications on some alien species of the European continent (Leppäkoski, 2002; Tedeschi et al., 2022). The most striking examples are the grey squirrel (Bertolino et al., 2014; Wauters et al., 2023), northern raccoon (Salgado, 2018; Stope, 2023), and muskrat (Kadlec et al., 2007; Gethöffe & Siebert, 2020).

One of the important documents of European attention was Recommendation 77 of the Standing Committee of the Bern Convention 'On the eradication of alien species...' (1999), which lists a number of species to be eradicated, including the species considered here: *Mustela* [=*Neogale*] *vison*, *Ondatra zibethicus*, *Myocastor coypus*, *Cervus nippon*, *Procyon lotor*, and *Nyctereutes procyonoides* (https://rm.coe.int/16807466df). In fact, the same set of species is discussed in the latest review on 'Invasive alien mammals of European Union concern' (Tedeschi et al., 2022). Invasive alien species are recognised as one of the five main drivers of biodiversity loss in the IPBES Global Assessment of Biodiversity and Ecosystem Services (Paris, 2019). That is, the problem of regulation is acute and is determined by the excessive presence of aliens in both urban and natural ecosystems, which causes significant damage to both the human economy and natural faunal communities.

As can be seen, the proportion of bagging is generally small and varies from 0.02% in the case of the muskrat to 27.5% for the raccoon, with average values for all species of the order of 3–6% (Table 5). This is an extremely small value, which is significantly less than the annual offspring and indicates that bagging measures actually do not change the natural population size of the introduced species. Moreover, the volume of bagging of introduced animals has changed little over the years, which means only one thing: the factor of licensed (by hunters) removal of animals from their natural populations does not play any role in restraining the processes of population dynamics. Even if it occurs, then its containment is due to the action of other factors (forage, predation, diseases, climate, etc.).

Table 5
Volumes of bagging of alien species from the list of game fauna according to the data of the state statistics of Ukraine '2tp-hunting' in comparison with data on species abundance

Species	Number of bagged animals by years*												Abundance	Bagging
	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	ave5	2021	%
Ondatra zibethicus	306	91	16	7	13	2	0	0	100	0	5	21	97072	0.02
Nyctereutes procyonoides	3723	3743	3394	3385	3483	3402	3482	2970	2938	2830	2332	2910	10571	27.53
Neogale vison	13	–	7	122	136	147	67	73	44	235	112	106	9314	1.14
Cervus nippon	175	215	145	170	155	211	236	270	263	217	204	238	4701	5.06
Dama dama	76	77	74	55	49	40	21	57	65	44	70	51	1369	3.75
Ovis gmelini	42	59	21	25	21	27	2	83	101	4	63	51	807	6.27

Note: * ave5 is the average value for the last five years (% bagging is calculated for this value).

It is also important to note that despite Ukraine's signing of relevant international agreements, in particular the Bern Convention, as well as the generally obvious problems with alien species and the deterioration of populations of vicarious native species, the regulatory situation has not changed in any way. Moreover, despite the clear demand for the eradication of alien species, there are significant restrictions on bagging of this group of species in Ukraine, and these restrictions are as effective and licensed as the hunting of aboriginals. It is obvious that the hunting economy should not support the population of alien mammals, even in closed natural areas, but in every way should contribute to the growth of aboriginal populations. Nevertheless, introduced species have become the priority of many hunting projects (Evtushevsky, 2012; Sheihas, 2023).

The same trend persists even in nature conservation activities. For example, in the 'Red Book of Ukraine' there are four obvious aliens among bats, besides, they are almost exclusive synanthropes: *Plecotus austriacus*, *Eptesicus serotinus*, *Pipistrellus kuhlii* (= *lepidus*), *P. pygmaeus*. The issue of the alienness of these species has been raised by us more than once (Zagorodniuk, 2006; 2019), but they are repeatedly included in the regional and national red lists of Ukraine, which discredits the very idea of protection, since the main form of human interaction with them is constant conflicts precisely due to their synanthropy. Similarly, in nature conservation, the topic of alienness is increasingly being ignored even in biosphere reserves. Thus, in the Danube Biosphere Reserve, the presence of muskrats is recognised as an important and desirable environmental factor; moreover, in the last year, according to the reports of numerous mass media, there were loud campaigns for the introduction of Indian buffaloes (*Bubalus bubalis*) and fallow deer (*Dama dama*), which the authors have already paid attention to (Zagorodniuk, 2023b).

In general, the situation with introduced species develops not towards their eradication, but towards reconciliation with the fact of their existence and moderate exploitation of their populations. The same applies to invasive species, whose appearance in the best traditions of the past is considered as 'enrichment' of the local game fauna and 'improvement' of hunting grounds, etc. Nothing has changed since the times when 'successful farmers' in 1930–1970 considered such 'improvements' as a priority form of natural resource management and as a key task not only for hunting farms, but also for nature conservation institutions. The beginnings of this in Ukraine were laid by the work of B. Fortunatov (e.g., Fortunatov, 1933), which is analysed in detail in the relevant biographical survey (http://doi.org/10.53452/nt1633). And this approach has remained unchanged over the years. And if the effects and abundance of herbivores (rodents, ungulates) can still be 'somehow' regulated, the effects of foreign predators (primarily mink, raccoon dog, and raccoon) remain uncontrolled.

Actually, the latter should become the object of special attention of game experts and hunters as those who could ensure the regulation of the presence of alien species by regulating the licensed shooting of game animals. However, the available experience shows that the objects of attention of hunters receive special support through direct protection and biotechnology, while species outside licences and even more so species from the Red Data Book become a headache for them, which it is better to get rid of. Therefore, the most expected result in the guardianship of the topic by hunters will be an increase in the proportion of alien species and the further extinction (including underestimation of survey data and eventually disappearance from survey results) of aboriginal species, especially those with a high conservation status, as it happened with the bison (*Bison bonasus*) (Parnikoza et al., 2010).

There are many direct and indirect impacts of the war on the fauna, both on native and invasive species, as well as on domestic animals, which have been the subject of special analyses (Kotov, 1924; Dudley et al., 2002; Lawrence et al., 2015). This topic is increasingly becoming a key concern for the conservation of biotic diversity in the world as a whole (Machlis et al., 2011; Hanson, 2018; Santini et al., 2023) and in Ukraine in particular (Zagorodniuk & Vyshnevskyi, 2022). However, in addition to the factor of war as a state and as a system of impacts on the environment and on forms of natural resource use, there are also impacts that directly change this environment or affect the biota, its composition, population viability and life cycles.

War is an extremely powerful factor of biota change, as it disrupts all conditions of the biota's existence and all established forms of nature management, and, in addition, there is an extremely high accidental mortality of animals, forced migrations and the emergence of numerous groups of unmanaged domestic animals (Zagorodniuk, 2024).

The examples of Kuhl's pipistrelle and the golden jackal expansions mentioned in the introduction are clearly occurring in the context of global warming, but can only partially be explained by climatic factors, which are significant in any case. In our opinion, the triggering mechanisms for the dispersal of both species can be considered to be military actions, both in the Balkans and in the Caucasus region, and we accept this scheme when analysing changes in the fauna and range dynamics of these species in Ukraine (Zagorodniuk & Vyshnevskyi, 2022; Zagorodniuk, 2024). Moreover, the years have only confirmed our assumption formulated 20 years ago that 'The main thing in the development of invasions was the northern direction, which coincides with two gradients: the degree of environmental disturbance and the scale of local and regional wars, which increase to the south' (Zagorodniuk, 2006).

This is exactly what is happening now with the extensions of expansion zones and successful introductions of all species considered herein, without exception, and in some cases the geography of such successes has reached the northern territories of Ukraine. Obviously, this is due to both significant climate warming and unidirectional (in geographical terms) changes of the biota: the centres of introductions and expansions are directed from south to north.

Details on the formation of the polemochore faunal assemblage (animals that have expanded their ranges due to factors of war) are presented in the review 'Fauna of War' (Zagorodniuk, 2024). Here, we note the most important trends related to introductions:

1) numerous feral individuals and groups of domesticated animals appear, including a wide spectrum of species, but the most no-table are domestic pigs (*Sus domesticus*), including those with offspring. The latter indicates not only the possibility of free existence, but also reproduction, with hybrids with the wild form (*Sus scrofa* s. str.), which leads to contamination of the gene pool, not to mention the well-known harmfulness of razorbacks; the lists of feral forms that are capable of forming hybrids with

natural populations also include feral domestic dogs (hybrids with wolves and jackals) and feral domestic cats (hybrids with wild cats). All of these are clear threats to biodiversity;

2) there are obvious escapes from captivity of a number of species that are not traditional domestic animals but are kept in some farms, such as coypu (*Myocastor coypus*), which have been repeatedly noted by the military and journalists in their reports. It is important to note that the share of such registrations reaches the same level of press coverage as the findings of other animals. Among these 'accidental' mammalian escapees are raccoons (*Procyon lotor*), degus (*Octodon degus*), teleutka squirrels (*Sciurus vulgaris exalbidus*) and other former 'pets' mentioned below (point 3);

3) there are regular escapes from breeding facilities, including deliberate forced releases (usually when the owners leave or occupiers behave irresponsibly) and escapes of animals as a result of the destruction of breeding facilities; this applies, in particular, to raccoons (Procyon lotor), as described above. This is one of the serious problems known as 'escapes from captivity', which have led to the formation of huge populations of many alien species, the damage from which is measured in terms of both economic and biodiversity losses (Diagne et al., 2021; Ahmed et al., 2022);

4) ongoing migrations of animals, including forced relocation under the influence of constant stress, escape from cage-type hunting farms, appearance in many areas where the species has not been previously seen, such as sika deer (*Cervus nippon*), and even exotic animals such as camels (*Camelus bactrianus*), etc. Such movements and appearances of animals in uncharacteristic habitats have been noted in various sources cited above more than once.

The previous cycles of research aimed at continuously 'refining' the composition of the fauna and the boundaries of species distribution, especially characteristic of the works of the entire 20th century, have gradually changed, which is the subject of several studies by the authors (Zagorodniuk, 2006, 2019; Lazariev, 2022). Finally, the changes concerned not only the aborigines. The time has come to recognise the dynamics of fauna, both the composition of local faunas and the distribution limits of certain species. Over the past two decades, many review papers have appeared on this topic for various groups of the Ukrainian fauna, including aquatic invertebrates (Son, 2019), fish (Kvach & Kutsokon, 2017), terrestrial vertebrates (Zagorodniuk, 2023b), and others. Almost all studies emphasise a significant increase in the frequency of alien species occurrence over time.

However, there are also specific climate impacts. Analysis of a large number of models shows that climate change is a significant factor in the dynamics of alien species' ranges, but there are specifics for certain taxonomic groups. In particular, unlike invertebrates and pathogens, which spread extremely quickly and widely, climate change in vertebrates is more likely to cause a decrease in the size of their ranges than an increase (Bellard et al., 2018). Obviously, this is fully applicable to mammals, especially terrestrial ones. However, overcoming barriers is easy for some mammals because of their ability to fly (bats), synanthropy (bats and rodents), or their amphibious lifestyle. Regarding the latter, this way of life ensures rapid expansion through river networks as natural corridors (Lazariev, 2023a) and the water canal system as artificially created econets. This is fully reflected in the expansion of two species such as muskrat and vison (American mink) that followed their introductions (see above).

An analysis of the literature shows, there have been obvious periods of cooling and warming. Several such waves have been de-scribed for the fauna of Ukraine, of which two warm phases in the 1930s and 2000s were key over the past 100 years (Zagorodniuk & Kharchuk, 2022). However, this happened many times before, as discussed in the cited publication; in particular, there was a warming wave in the 1830s and 1850s followed by a prolonged cooling. Among the examples of remarkable changes in the mammalian fauna, the latter work also mentions the introduction of the coypu (*Myocastor coypus*). Coypu has a long history of introductions in Ukraine, which stretches back to the early 1930s (discussed in the journal 'Ukrainian Hunter and Fisherman' in 1931, No. 4), i.e. the first warm wave. All further reports of the 1950s–1990s concerned the registration of individual escapees, for whom it was repeatedly noted that they could not survive the winter, even in the south, in the Syvash (Hrinchenko & Dulitsky, 1984). However, in the last 10–15 years, the situation has changed, as evidenced by the above data. This is an example of an introduced species that was limited by low winter temperatures and ice cover. As we have noted many times, the number of reports of successful introductions has been increasing in recent years, including as a result of deliberate introductions and other forms of escapes from captivity (e.g., due to military operations).

The climatic component is important in considering the expansion of an invasive species (primarily escapees) such as the raccoon in Europe (Cunze et al., 2023). Its previous introduction in the Pripyat Basin (southern Belarus on the border with Ukraine) in the 1950s was ultimately unsuccessful and the species disappeared (Savarin, 2007). However, a process of population recovery has now begun, probably due to escapes (see above) in addition to the rapid expansion of the species towards Ukraine from the west (Nikolaichuk & Zagorodniuk, 2019). These three facts, namely the reappearance in Belarus, cases of new successful escapes from captivity in Ukraine, and continued expansion from the west, are evidence of the beginning of the formation of local populations in Ukraine, which is taking place against the background of global warming. It is clear that these processes are coordinated not only with the geography of the species' introduction into culture (and the presence of escapes), but also in accordance with global climate change (Louppe et al., 2019).

It is important to note that a number of expansions (without introductions) in the local fauna clearly occurred during the last period of climate warming. Such phenomena are discussed in more detail in our 2022 review (Zagorodniuk & Kharchuk, 2022). Examples of such changes include wide expansion to the north of the golden jackal (*Canis aureus*), soprano pipistrelle (*Pipistrellus pygmaeus*), and the mound-building mouse (*Mus spicilegus*), and the formation of wintering groups of previously obligate migratory bat species, including the common noctule (*Nyctalus noctula*) and the parti-coloured bat (*Vespertilio murinus*). Such peculiarities of population dynamics were described earlier (Zagorodniuk, 2019) and require further analysis. For example, it is very incorrect to explain the rapid dispersal of the jackal (only) by gradual climate warming; other factors, including wars, were probably at work (Zagorodniuk & Vyshnevskyi, 2022). Of course, similar changes have occurred in the past, but only now have they reached the level of significant changes in the structure of zonal faunal assemblages. It is noteworthy that all similar processes occurred during the previous thermal optimum of the 1930s, as evidenced by some facts, such as the hibernation of migratory bats in hollows in Nizhyn (Velykaniv, 1930), but in general they are poorly documented.

Thus, all five factors discussed here, including the availability of suitable habitats, population control measures, the impact of hostilities, and climate change, influence the spread of introduced species. When these factors coincide favourably, introductions demonstrate not only the successful formation of local populations, but also a marked increase in numbers and expansion beyond the areas of introduction. This means that species move from the AS1c alien category ('local introductions') through the AS2c category ('successful invasive species') to the AS3c category ('introduced species with widespread expansion'). In other words, the model of population development is described by an initial local introduction followed by regional and subsequent widespread expansion, when in many regions the species becomes invasive that came 'on its own' without secondary introductions.

Conclusions

The mammal introductions carried out in Ukraine have been mostly successful, which is evidenced by the effective selection of species. The introductions resulted in an increase by almost 10% of the actual species composition of the fauna, primarily among large-sized amphibious rodents (muskrat, partially coypu), carnivores (vison, raccoon), and some ungulates (sika deer). Other more terrestrial species have shown little progress, which is primarily due to the small size of available spatial niches (rabbit, onager, horse, mouflon). Almost all of them are species from the group of 'game animals'.

Most of the introduced mammal species showed a rapid increase in abundance, including in comparison with the native ecologically similar species; in particular, a significant increase was shown by a) muskrat, *Ondatra zibethicus*, simultaneously with the decline of the native *Arvicola amphibius*, b) sika deer, *Cervus nippon*, simultaneously with the decline and subsequent freezing of the numbers of the native *Cervus elaphus*, c) American mink, *Neogale vision*, simultaneously with the decline of the native *Mustela lutreola*.

Most species have developed wide expansions after introductions, i.e. independent dispersal from the introduction sites has taken place, which is especially evident in semi-aquatic species such as muskrat and American mink. Some of the introduced species are distributed more across river basins or separate regions of introduction, and practically none of them form a range that corresponds to the natural (biogeographical) zonation. In terms of biogeographic zones, the most favourable conditions are found in the foothill areas of the Carpathians and Crimea, forest-steppe regions and intrazonal complexes along river valleys.

There is a clear increase not only in the number of alien species, but also in their total abundance, which has become almost equal to the numbers of ecologically similar species of the native core. It is largely due to the successful incorporation of these species into guilds. The analysis of guilds by the size parameters of animals shows a very effective structure for such entries, particularly in the arvicolid guild (semi-aquatic herbivorous rodents) and canid guild (large carnivorous canid families), as well as the ungulate guild (herbivorous species of open spaces). The most problematic was the introduction of new species into the mustelid guild, which led to the extinction of some of the native species.

Regulatory measures by removing part of the population by hunters have proven to be extremely ineffective. The proportion of the population of alien mammals bagged by hunters every year averages 3–6%, which is 1–2 orders of magnitude less than the annual population growth. Moreover, the special attention of land users to alien species (and the support of their populations) and the continued allowance of hunting on introduced species (primarily outside of cage farms) make this group invulnerable and even privileged, often more protected than rare (and endangered) species of native animals.

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