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ESTIMATING THE POPULATION DENSITY OF EURASIAN LYNX IN THE UKRAINIAN PART OF THE CHORNOBYL EXCLUSION ZONE USING CAMERA TRAP FOOTAGE

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Eurasian lynx, Chernobyl Exclusion Zone, camera trap, population census, large carnivore, Europe

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Abstract

The study reports the first estimation of the Eurasian lynx population inhabiting the Ukrainian Chornobyl Exclusion Zone (CEZ, 2600 km^2) in 2013–2018. Although lynx were once common in this region, anthropogenic impacts reduced their numbers substantially by the 19th century, leaving lynx as only occasional visitors to the area. In 1986, after an accident on the Chornobyl NPP, the human population was removed from the areas affected by radioactive contamination, and regular economic activity was stopped there. As a result, a gradual recovery of the lynx population was observed. Assessments of the given study are based on camera trap data obtained from wildlife studies conducted in 2013–2018 over nearly 30% of total CEZ area. The number of locations where the camera traps worked simultaneously ranged from 5 to 89. Lynx was recorded 302 times, including 125 observations of 50 identifiable individuals. The total size of the lynx population was estimated to be approximately 53 to 68 individuals of all sex and age groups. For the identified lynx, sex was defined for 22 individuals: 6 females and 16 males. Eleven of 50 identified individuals were cubs. Over the whole period 6 family groups were recorded, 5 of which were females that had 2 cubs, and one a female with a single cub. Most of the identified lynx (33 of 50) were each recorded in one location only. In those cases when the individuals were repeatedly observed in two or more locations (up to 6), the maximum distance between locations ranged from 1 to 23 km (mean distance = 1.9 km). The density of animals was approximately 2.2–2.7 individuals per 100 km^2, which is comparable to other areas of Europe where conditions are favourable for this species. Whilst only a preliminary estimate, our results indicate that 32 years after the Chornobyl NPP accident, the CEZ has one of the highest lynx populations in Ukraine. Conditions for lynx are favourable in the CEZ because it has abundant prey species (roe deer and red deer), high forest cover (more than 63%), absence of a residential human population, no agricultural activity, a low level of disturbance from other human activity, and the area has protected status. The recovery of lynx in the CEZ demonstrates the conservation benefits that even unmanaged re-wilding can achieve.

Cite as

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Оцінка щільності популяції рисі євразійської в українській частині Чорнобильської зони відчуження з використанням фотопасток

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Резюме. В роботі представлена перша оцінка розмірів популяції рисі євразійської, що мешкає в українській частині Чорнобильської зони відчуження (ЧЗВ, 2600 км^2), за станом на 2013–2018 роки. Хоча у минулому рись була звичайною у регіоні, антропогенний вплив суттєво скоротив її чисельність ще до XIX ст., зробивши її лише випадковим відвідувачем території. У 1986 р., після аварії на Чорнобильській АЕС, людей евакуювали з земель, вражених радіоактивним забрудненням, а звичайну господарську діяльність припинили. Як результат, спостерігалося поступове відновлення населення рисі. Оцінки, наведені у даній статті, ґрунтуються на аналізі фотоматеріалів з фотопасток, отриманих у 2013–2018 роках у дослідженнях диких тварин, що охопили близько 30 % загальної площі ЧЗВ. Кількість точок, де одночасно працювали фотопастки, варіювала від 5 до 89. Всього рись реєстрували 302 рази, включаючи 125 раз 50 індивідуально ідентифікованих особин. Загальний розмір популяції оцінено близько 53–68 особин всіх статево-вікових груп. Із 22-х дорослих рисей з визначеною статтю самки складали 6 особин, самці — 16. Одинадцять з 50 ідентифікованих особин були дитинча-цьоголітки. За весь період зареєстровано 6 сімейних груп, в 5-ти з яких у самки було по 2 дитинча, в одній – одне. Більшість ідентифікованих рисей (33 з 50) реєстрували лише в одній точці. У тих випадках, коли їх повторно реєстрували у двох або більше точках (до 6), найбільша відстань між точками складала від 1 до 23 км (в середньому 1,9 км). Щільність рисей складала 2,2–2,7 особин на 100 км^2, що збігається з щільністю в інших регіонах Європи, зі сприятливими для виду умовами. Хоча це попередні оцінки, результати свідчать, що за 32 роки після аварії на Чорнобильській АЕС у ЧЗВ сформувалася одна з найбільших популяцій рисі в Україні. Сприятливість місцевих умов визначається багатством видів-жертв (сарна європейська, олень шляхетний), значним лісопокриттям (понад 63%), відсутністю людського населення і сільськогосподарської активності, низьким рівнем неспокою від інших видів людської діяльності, і тим, що територія має охоронний статус. Відновлення рисі у ЧЗВ демонструє природоохоронну користь, яку надає навіть звичайне здичавіння земель без управління з боку людини.

Ключові слова: рись євразійська, Чорнобильська зона відчуження, фотопастка, оцінка популяції, великі хижаки, Європа.

Introduction

Eurasian lynx, *Lynx lynx* (L., 1758), were once common in Polissia (north and north-west Ukraine), including lands which are now part of the 2600 km^2 Ukrainian Chornobyl Exclusion Zone (CEZ) [Kirikov 1960; Sokur 1961]. Deforestation and direct persecution resulted in the species becoming rare during the 19th century and, in the 20th century lynx were only occasional migrants into northern Ukraine with the main breeding populations being to the north in Belarus [Heptner & Naumov 1972; Matyushkin & Vaisfeld 2003; Savitsky *et al.* 2005]. Poaching (illegal killing), fragmenting of the natural landscape and depletion of food reserves were considered to be the main reasons for the decline of the species in Ukraine [Shkvyria & Shevchenko 2009]. The situation began gradually to improve in the 1990s, when population growth and spread were reported both in Belarus [Savitsky *et al.* 2005; Deryabina 2008] and in northern Ukraine [Zhyla 2002]. Social and economic problems (in part because of the break-up of the Soviet Union) in Ukraine and Belarus in the late 1980s and early 1990s could have been a precursor for lynx recovery. Decline of forestry and agriculture activity, and a migration of rural populations decreased pressures on lynx numbers. The most notable change was in the territories affected after the 1986 Chornobyl accident, from which all the human population was removed and regular economic activity was stopped. In the 2170 km^2 Polessky State Radioecological Reserve of Belarus (PSRER; established in 1988 in the Belarussian part of the Chornobyl exclusion zone) the first records of lynx were reported in 1989, 3 years after the accident [Deryabina 2008]. By 1996–1997 researchers reported about 10–12 individuals in

PSRER, rising to 28 by 2001 and 30–40 by the mid-2000s [Deryabina 2008]. The first reports about lynx in the Ukrainian CEZ were in the early 1990s [Gashchak *et al.* 2006]. The number of reports and the geographical spread of lynx observations in the Ukrainian CEZ gradually grew. The local ranger service (N. G. Samchuk (Enterprise 'Chornobyl Les') pers. comm.) stated that about 18 individual lynx had been counted in the CEZ in winter 2000. Subsequently, Zhyla (2002) reported about 10 lynx inhabiting 500 km^2 of 'Chornobyl lands' in the north of Kyiv Oblast, but the article did not explain how the data had been obtained nor from which area of CEZ they had been collected. There were other unrecorded communications about sightings and even poaching of lynx, however no comprehensive studies were conducted. It is likely that the number of lynx was low in the early 2000s; the species was not recorded by camera traps (CT) deployed in the CEZ 2001–2005 [Gashchak 2008].

In 2013–2018 we resumed studies of fauna in CEZ using CT. The main goal was species composition and relative abundance of mammals on the areas having potential environmental value [Gashchak *et al.* 2016; 2017; Gashchak 2018; Gashchak & Paskevich 2019]. Some studies were also dedicated to wildlife diversity and abundance in relation to radioactive contamination of habitats [Wood & Beresford 2016; Beresford *et al.* 2021]. The study designs and conditions of the research projects differed. However, for the first time numerous data about Eurasian lynx in the CEZ were obtained due to these studies. The goal of this article is to summarise information about lynx obtained from these various studies in 2013–2018, and to produce a preliminary estimation of the lynx population size in the CEZ.

Materials and Methods

Study area. The CEZ is situated in a central part of northern Ukraine, largely between the rivers Prypiat and Uzh, and occupies approximately 2600 km^2. According to the natural-territorial zoning [Marynych *et al.* 1985] this is a Kyiv sub-province of the Ukrainian Polissia. The climate is continental; data from the Chornobyl meteorological station shows the average (1990–2020) air temperature in January was –3.3°C and in July +20.2°C, the average annual precipitation was 616 mm. There are normally periods of snow cover from the second half of November until the beginning of March; this rarely exceeds 10 cm and melts several times during winter. The landscape topography is relatively flat with no high hills. Most land is between 115 and 140 m above sea level, the floodplain of the Prypiat river and its western bank are lower at 105–120 m. However, since the local landscapes were formed by ancient glaciers, there are a number of sandy ridges and dunes, and swampy lowlands. During the study period, approximately 63% of the total CEZ territory was forest; most of which (60% of all forests) was dominated by Scots pine (*Pinus sylvestris*)[1]. Open habitats (i.e. former arable lands, meadows) can be found throughout the CEZ but are reducing due to natural reforestation (succession). The forested area in 2013–2018 was 30% larger than that prior to 1986. Most of the remaining former agricultural land is now scrub with young trees, bushes, and sparse forest. The most common tree species, apart from Scots pine, are birch (*Betula pendula*, *Betula pubescens*), aspen (*Populus tremula*), and alder (*Alnus glutinosa*, *Alnus incana*). Birch species occupy up to 25% of the total forest area and more than 55% of areas of post-accidental reforestation. The once common deciduous forests in the area, oak (*Quercus robur*), hornbeam (*Carpinus betulus*), ash (*Fraxinus excelsior*), now comprise only 4–5% of the total CEZ territory, and no more than 7–8% of the forested area. The rivers Uzh and Prypiat have wide (up to 5–7 km) floodplains with numerous small lakes, oxbows, and marshes. Over approximately half of the territory there is a network of small shallow streams and drainage channels. In summer a number of the small water bodies and swamps dry up. In the south-eastern part of CEZ there is an upper part of Kyiv Reservoir of the Dnieper River, with numerous reed islands and channels. Before 2016–2017 in the central part of the CEZ there was the large (22 km^2) artificial cooling pond of the Chornobyl NPP. However, starting in

[1] Here and further, data on forests of the CEZ are given according the dataset of the Ukrainian state engineering forest management production association: Development Project for the Forestry of the State Specialized Integrated Enterprise 'Chornobyl Puscha.' Integrated expedition. Irpin, 2006.

2014, this has been drawdown (drained) leaving a network of small lakes with riparian habitats and marshlands dominated by reeds (*Phragmites australis*) or thickets of different willow species (*Salix* sp.). The total area of marshes and running and standing water bodies during the study period amount to no more than about 10% of the total area of the CEZ. Although there were nearly 80 settlements in the CEZ together with industrial areas these have mostly been abandoned since 1986. People are only in some central locations of the CEZ, and in a few villages of southern and western sectors. Almost all are employees of local organizations (totaling up to 3500–4000 persons in 2013–2018, with 1500–2500 people daily in the CEZ). Agricultural activity in the CEZ is absent. Active forestry is limited to a few small sites and also management to prevent fires. Industrial activity is located at a few small sites and does not impact on surrounding habitats. Traffic is also limited and largely restricted to a few roads. Whilst tourism has been increasing in the CEZ, with an estimate of >70 000 visitors in 2018[2], this activity has to date been restricted to a few areas. In 2016, the Chornobyl Radioecological Biosphere Reserve was established in the CEZ; the Decree of the President of Ukraine (2016)[3] assigned 87.6% total area of CEZ to the Reserve (all of the CEZ except for the central areas around the Chornobyl NPP).

Study sites. The data discussed in this paper were obtained from several research projects using motion-activated camera traps: 1) 'Research and identification of the exclusion zone areas with the most valuable natural systems and worthy of the highest conservation status, and their passporting' (2013–2018, supported by the Ministry of Ecology and Natural Resources of Ukraine); 2) the UK-funded TREE project (2014–2016, http://tree.ceh.ac.uk); and 3) the UK-funded RED FIRE project (2016–2017, https://ceh.ac.uk/redfire). Each project had its own research design, study sites and approaches for the wildlife investigation; in the few cases (8 of 390) the camera were deployed in the same locations as in a previous project. The projects assessed all fauna (generally focussing on medium/large mammals) and were not designed to get quantitative assessments of abundance and density of Eurasian lynx across the CEZ.

The studies were carried out at sites, some relatively small (20–175 km^2; 2.5–7.4 km radius), in different areas of the CEZ. Therefore, the study results reflect the situation at those sites (representing about 30% of the total CEZ area) and during the periods when the camera traps were operating. In total, there were eight study sites (see Fig. 1, Table 1).

Table 1. Total number of CT locations (n) and trap-days (TD) at each study site by years, and the effective trapping area (ETA) of the sites

Таблиця 1. Загальна кількість точок розміщення фотопасток (n) і пастко-діб (TD) для кожної дослідної ділянки по рокам, і ефективна площа реєстрації (ETA) для кожної ділянки

Study site	ETA, km^2	2013 n/TD	2014 n/TD	2015 n/TD	2016 n/TD	2017 n/TD	2018 n/TD	Total n/TD * (2013–2018)
1	124.8		14 / 530	95 / 4881	24 / 804		1 / 43	96 / 6257
2	170.0	2 / 212	24 / 1548	99 / 5848	37 / 4615	1 / 203	5 / 903	120 / 13329
3	174.4		14 / 470	95 / 4792	22 / 787		9 / 1396	105 / 7444
4	53.3	5 / 749	5 / 661				3 / 735	8 / 2145
5	116.6		1 / 154	2 / 362	19 / 2348	25 / 4412	14 / 2522	35/ 9797
6	88.2						14 / 3347	14 / 3347
7	60.2			3 / 498	3 / 672			3 / 1170
8	23.8					7 / 375	7 / 1928	7 / 2303

*The annual CT location and TD numbers do not sum to the total as some sites were used across multiple years.

Note: The total combined ETA of all sites was 811 km^2 (approximately 30% of the total area of the CEZ (2600 km^2)). Camera trap images are available in the accompanying dataset [Gashchak *et al.* 2022]).

[2] See: https://www.statista.com/statistics/1231428/number-of-tourists-in-chernobyl-exclusion-zone/

[3] Decree of the President of Ukraine 'About establishment of Chornobyl radiation and ecological biosphere reserve', No. 174/2016, 26.04.2016.

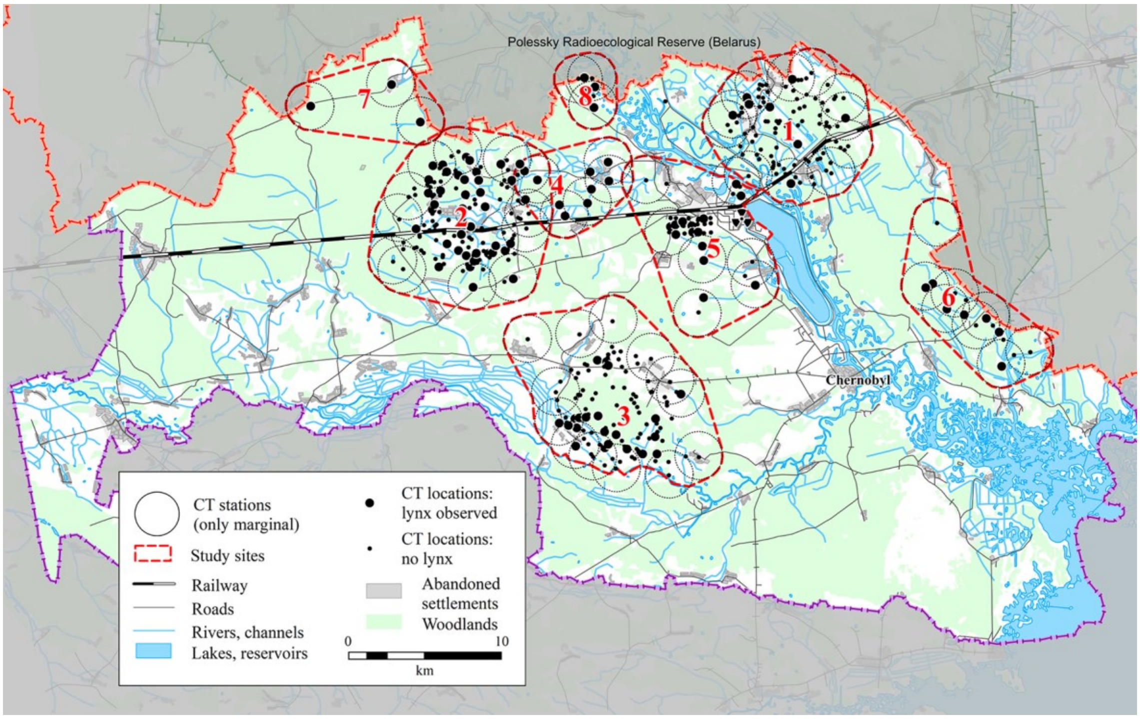

Fig 1. Study sites and CT locations where the camera traps were deployed in 2013–2018.
Рис. 1. Дослідні ділянки і точки розміщення фотопасток у 2013–2018 роках.

We estimated the total abundance and density of lynx relative to the total effective trapping area (ETA) at each study site. The ETA is a polygon which comprises all the camera trap locations for a given study site. The boundaries of the ETAs were defined using a circle with a radius of 0.5 MMDM, with its centre on the camera trap location, was drawn. MMDM is the mean maximum distance of re-photographing of identified individuals if observed at different camera locations; in the given study MMDM equals 1.91 km (Table 2). Circles centred on the marginal camera trap locations were used to define the boundary of the ETA (see Fig. 1). This approach follows that used in previous studies for a range of animals, including lynx and other large cats [Di Bitetti *et al.* 2006; Silver *et al.* 2004; Karanth & Nichols 1998].

In total, we deployed camera traps at 390 locations, and they operated over 46 830 trap-days. Detailed descriptions of the settings are presented in the accompanying datasets [Gashchak *et al.* 2022; Barnett *et al.* 2022].

Camera traps. The majority of the cameras used were Ltl Acorn 6210 MC (n = 60), although several other models were also deployed in the study: Ltl Acorn 5210A (n = 1), Ltl Acorn 6210 MG (n = 9), Browning BTC5 (n = 2), Browning BTC-7FHD-PX (n = 10), Bushnell 119437 (n = 1), Bushwhacker Big Eye D3 (n = 1), CCBetter (n = 4), DLC Covert Red40 (n = 2), DLC Covert Red40Ex (n = 1), ScoutGuard 880MK (n = 1), ScoutGuard 882MK (n = 1), and Weltar 8210A (n = 1), the potential settings and abilities of which differed. With few exceptions, the CT had the following settings: still pictures 3–5 MB, three pictures burst per triggering, 0–5 sec delay between triggering, maximal possible infra-red flash power. Recovery time of the various CT differed from 3 to 10 sec, therefore there was the potential to miss some animals between triggerings. As sensor sensitivity is temperature dependent, where required, it was set dependent on season: low/normal sensitivity in cold seasons; high/normal sensitivity in warm seasons. Some of the cameras (Browning) adjusted sensitivity automatically. Subsequent to November 2014 most of CT were Ltl Acorn 6210MC (up to 45 being deployed in the TREE and RED FIRE projects). From April 2018 we used Bushwhacker Big Eye D3 (n = 1) and Browning BTC-7FHD-PX (n = 10) cameras in video mode; from March to June 2016 cameras deployed for the TREE project were also set to record video.

Normally we deployed the CTs at a site for up to 10–12 months. However, the TREE project's CTs were deployed for 8 to 9 weeks, after which they were moved to new random locations within the same study site (a more detailed description of the TREE CT study can be found in Gashchak *et al.* [2016]. No bait was used during any of the studies.

CT mounting. Normally the CTs were deployed within 3–10 m from an area where animals were likely to be encountered. They were mounted on trees, or occasionally on specially made poles, at heights of 0.5–1.1 m above the ground depending on local topography. Mostly the CT locations were selected on well-marked pathways (field or forest roads), the intersection of such pathways, or on bridges over channels; the general location of TREE camera locations were randomly selected. In some cases, a relatively high risk of the CT being seen by people was assumed and therefore the CTs were concealed (e.g. covered with bark). To prevent false activations caused by sunlight, the CT mostly faced north or towards thickets to shield them from direct sunlight. Tall grass, bushes and thin tree branches were removed as appropriate from the detection zone in front of the CT to reduce false activation. As a rule, cameras were oriented parallel to the ground, but the exact orientation depended on local topography, camera height and trail location.

In most cases when setting up each camera trap, up to 20 measuring poles (1 m high and with clear markings at every 20 cm) were laid out in front of the camera. The camera was activated to capture an image of the poles *in situ* and the poles were then removed. Later, images of the poles and animals were overlaid using graphic software so that animal dimensions could be estimated (Fig. 2). The height of lynx at the shoulder and hind-quarters were estimated with an approximate accuracy of ± 5 cm. These values were used to aid the identification of individuals.

Footage processing. In total, 1570 still photographs and 23 videos were obtained as a result of lynx activating a CT. Image quality varied depending on CT model, features of the particular CT, light, angle, and behaviour of the animals.

Fig 2. An example of the overlapping an image with the measuring poles upon an image with a lynx.
Рис. 2. Зразок накладання фотографії з калібрувальними жердинами на фотографію з риссю.

Identification of lynx was based on the following characteristics:

1) Unique coat spot patterns (based on the images presented in Dulà *et al.* (2021), we assumed that fur patterns of lynx were generally similar on their left and right sides) (Figs 3–4);

2) Relative size and proportions of the body;

3) The place and time of other recordings thought to be the same individual (e.g. the same individual could not be recorded at distant sites at similar times);

4) Sex and age.

Where identifiable features (spot pattern, sex, age, size, etc.) were evident allowing subsequent recognition of the lynx, the animal was given a unique code (e.g. p0024-1). Where there were no readily identifiable features the animal was not allocated an ID code.

Approaches to the data analysis. It was assumed *a priori* that lynx have seasonal changes of activity and territorial behaviour [Belotti *et al.* 2013; 2018; Ogurtsov *et al.* 2018; Podgorski *et al.* 2008; Schmidt 1999], therefore the indices of relative abundance were estimated by calendar month.

In this paper the following terms are used: 1) 'event'—CT capture of one or several individuals, 2) 'record'—same as 'event' but for each individual separately if there were several animals per event.). Records (i.e. observations of an individual animals) were used in the estimation of relative abundance. Relative abundance of lynx was estimated from the record frequency of lynx either per month or year at a given CT location normalised to 100 trap-days (TD):

$R_i = \frac{n_i}{TD_i} \times 100$, where (1)

R_i—frequency of a lynx per month (or year) at CT location *i* per 100 *TD*, n_i—number of records over a given month (or year) at CT location *i*, TD_i—number of TD over month (or year) in CT location *i*. Camera locations where lynx were absent for a given month were included in the analyses (i.e. $R_i = 0$).

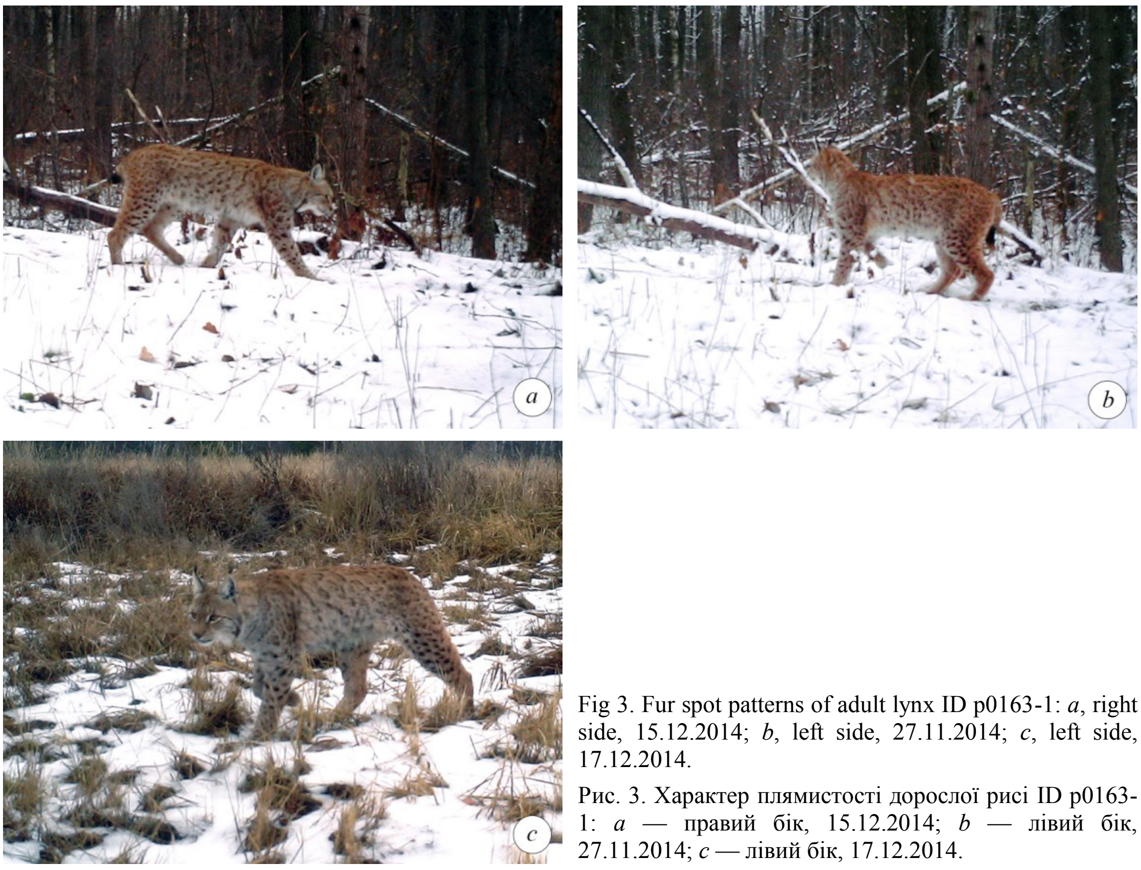

Fig 3. Fur spot patterns of adult lynx ID p0163-1: *a*, right side, 15.12.2014; *b*, left side, 27.11.2014; *c*, left side, 17.12.2014.

Рис. 3. Характер плямистості дорослої рисі ID p0163-1: *a* — правий бік, 15.12.2014; *b* — лівий бік, 27.11.2014; *c* — лівий бік, 17.12.2014.

Fig 4. Different types of fur spot patterns in lynx in the CEZ: *a*, male p0273-1, 6.08.2015; *b*, male p0144-1, 13.07.2013; *c*, male p0385-1, 8.02.2018; *d*, male p0167-1, 7.04.2014.

Рис. 4. Різні типи плямистості рисі у ЧЗВ: *a* — самець p0273-1, 6.08.2015; *b* — самець p0144-1, 13.07.2013; *c* — самець p0385-1, 8.02.2018; *d* — самець p0167-1, 7.04.2014.

Results

During the entire research period there were 265 events and 302 records of lynx, including 125 records of 50 identified individuals; in 177 cases it was not possible to identify the lynx. A list of the identified lynx is presented in Table 2; all individual data, including the majority of the trap camera photographs, from the study can be found in Gashchak *et al.* (2022). About 30% of all records were obtained in February–March, the mating season of lynx in this part of Europe [Heptner & Naumov 1972; Naidenko 2019; Schmidt 1999; Jedrzejewski *et al.* 2002].

For the identified lynx, sex was defined for 22 individuals: 6 females (presence of cubs) and 16 males (visible testis, or male urine marking behaviour). These were either mature or individuals older than 1 year (males only). Eleven of 50 identified individuals were cubs (immature, <1 year old).

For most events (237 of 265, or 89%) single animals were recorded. In eight cases (3%) two individuals were recorded per event, including for: five events—female with a cub; two events—2 of 3 members of the family group (female and two cubs); one event—two individuals of unknown gender and age. Three individuals per event were recorded 15 times (6%), almost always—female with two cubs, and just one event when sex and age of three individuals were not defined. Four individuals per event were recorded only once: an adult male plus a female with two cubs (observed in March 2014). In total, we recorded six identifiable family groups: one group of a female and one cub, and five groups of a female with two cubs (Table 3, Fig. 5). At site 4, 40% of total records and 66% of observations of identified individuals were for one female (p0166-1) with two cubs.

Table 2. Summary data for identified individual lynx including maximum distances of recapture in 2013–2018
Таблиця 2. Зведені дані щодо ідентифікованих особин рисі, включаючи найбільшу відстань повторної реєстрації у 2013–2018 роках

Animals recorded more than once							Animals recorded only once			
Ind. ID	Sex / age	Locations/ records	Max distance between observations, km	Month / year of the first record	Month / year of the last record	Days between the first and last record	ID code	Sex / age	Locations / records	Month / year of the first record
p0166-2	imm	6/14	14.5	08/2013	12/2015	851	p0024-2	imm	1/1	11/2014
p0141-2	F	3/3	10.6	04/2014	12/2014	269	p0031-1	M	1/1	06/2016
p0179-1	M	3/5	1.6	11/2017	08/2018	256	p0075-1	M	1/1	05/2016
p0163-1		3/4	3.3	11/2014	07/2015	235	p0086-1	M	1/1	08/2017
p0166-1	F	3/12	3.4	08/2013	03/2014	213	p0104-1	F	1/1	11/2016
p0166-3	imm	3/10	3.4	08/2013	03/2014	208	p0104-2	imm	1/1	11/2016
p0137-1	F	2/3	2.0	07/2013	07/2015	725	p0104-3	imm	1/1	11/2016
p0273-2	M	2/3	23.0	01/2015	03/2016	424	p0108-1	M	1/1	03/2016
p0257-1		2/3	3.0	07/2017	09/2018	405	p0134-1	F	1/1	01/2015
p0102-1	M	2/4	3.5	10/2014	08/2015	310	p0134-2	imm	1/1	01/2015
p0385-2	F	2/4	1.8	07/2018	08/2018	41	p0134-3	imm	1/1	01/2015
p0024-1	imm	2/2	1.6	11/2014	12/2014	34	p0137-2	imm	1/1	07/2013
p0069-1	M	2/2	2.3	01/2015	02/2015	22	p0141-1		1/1	11/2013
p0067-1	M	2/2	1.0	06/2015	06/2015	10	p0172-1		1/1	03/2014
p0179-2		2/2	12.9	09/2018	09/2018	2	p0172-2	M	1/1	05/2014
p0385-3	imm	2/3	1.8	08/2018	08/2018	1	p0182-1		1/1	02/2015
p0385-4	imm	2/3	1.8	08/2018	08/2018	1	p0261-1		1/1	06/2017
p0273-1	M	1/2	0.0	08/2014	08/2015	369	p0270-1		1/1	12/2016
p0394-1	M	1/2	0.0	09/2018	10/2018	56	p0270-2		1/1	12/2016
p0144-1	M	1/4	0.0	07/2013	08/2013	40	p0344-1		1/1	01/2016
p0167-1	M	1/3	0.0	03/2014	04/2014	30	p0382-1		1/1	07/2015
p0215-1		1/3	0.0	07/2015	08/2015	29	p0385-5		1/1	06/2018
p0385-1	M	1/2	0.0	02/2018	02/2018	18	p0399-1		1/1	08/2018
p0273-3		1/3	0.0	05/2015	05/2015	5	p0427-1		1/1	05/2018
							p0438-1		1/1	11/2018
							p0443-1	M	1/1	06/2018

Note: F—adult female, M—male (>1 year old), imm—immature individual (<1 year old).

Table 3. Records of family groups (F—female, Imm—cub(s)) at study sites in 2013–2018
Таблиця 3. Знахідки сімейних груп (F — самка, Imm — дитинча) на дослідних ділянках у 2013–2018 роках

Site	2013	2014	2015	2016	2017	2018
1	–	n/r	n/r	n/r	–	n/r
2	F: p0137–1, Imm: p0137–2	F: p0141–2, Imm: p0024–1,2	F: p0134–1, Imm: p0134–2,3	F: p0104–1, Imm: p0104–2,3	n/r	n/r
3	–	n/r	n/r	n/r	–	n/r
4	F: p0166–1, Imm: p0166–2,3	F1: p0166–1, Imm: p0166–2,3; F2: n/id–1,* Imm: n/id–2*	–	–	–	n/r
5	–	n/r	n/r	n/r	n/r	n/r
6	–	–	–	–	–	F: p0385–2, Imm: p0385–3,4
7	–	–	n/r	n/r	–	–
8	–	–	–	–	n/r	n/r

Note: *Possible that these animals were Female p0137-1 and cub p0137-2, but we cannot be sure. n/r—no records.

Fig 5. Family groups of lynx: *a*, female p0137-1 with one cub, 24.07.2013; *b*, two grown up cubs of female p0166-1, 3.02.2014; *c*, female p0385-2 with two cubs, 17.08.2018.

Рис. 5. Сімейні групи рисі: *a* — самиця p0137-1 з одним рисеня, 24.07.2013; *b* — двоє підрослих рисенят самки p0166-1, 3.02.2014; *c* — самка p0385-2 з двома рисенятами, 17.08.2018.

Discussion

Whilst the studies from which the lynx photographs were obtained were not conducted to enable estimates of population size in the Ukrainian CEZ, they do enable us to make an assessment.

Lynx is an animal with a land tenure system, and at optimal conditions adult individuals appear to have site fidelity, keeping a certain home range [Jedrzejewski *et al.* 1993; 1996; 2002; Schmidt 1998; Matyushkin & Vaisfeld 2003]. The size of the home range of lynx in the regions of Europe with conditions similar to the CEZ (i.e. Belarus, Lithuania, Poland, Bohemian Forest of the Czech Republic and Germany) depends on sex, age, body mass, abundancy of prey, forest cover, and disturbance [Filla *et al.* 2017; Belotti *et al.* 2015; Jedrzejewski *et al.* 1996; Matyushkin & Vaisfeld 2003; Schmidt 1998]. The home range size of family groups (female with cubs) ranges from 40 to 110 km^2 in the first months of the cubs life, and up to 80–170 km^2 in autumn–winter when the cubs follow their mother. Adult males roam over 90–250 km^2. Immature individuals (subadults (1–2 years old)) have a 40–55 km^2 home range. Radiotelemetry of individuals of different age and sex showed the home ranges are not tied lifelong to a particular territory [Jedrzejewski *et al.* 1996; Schmidt 1998]. Immature individuals may initially keep largely to their mother's home range, but subsequently they adopt their own home ranges dispersing 5–130 km from that of their mother with an increased total area [Jedrzejewski *et al.* 1996; Schmidt 1998; Zimmermann et al 2007; Weingarth *et al.* 2012]. However, an overlap of the home ranges of different individuals is common if conditions are optimal, and does not depend on age, sex, or affinity [Jedrzejewski *et al.* 1996; Schmidt 1998; Zimmermann et al 2007]. Therefore, there is the possibility of recording several individuals within a relatively small area who may not be related.

In neighbouring Belarus, lynx density has been reported to vary from 1.2 to 5.4 individuals/100 km^2 [Sidorovich 2006; Kozlo 2003], in Lithuania—2.6–8.4 individuals/100 km^2 [Bluzma 2003], in Bialowieza Forest (Poland)—3.6–5.0 individuals/100 km^2 [Jedrzejewski *et al.* 1996]. Only where the species is relatively rare its density decreases to 0.1–1.0 individuals/100 km^2 [Belotti *et al.* 2015; Jedrzejewski *et al.* 1996; Matyushkin & Vaisfeld 2003]. Many researchers note that lynx density depends on the characteristics of the area. The highest values (5–10 individuals/100 km^2) are found in areas with a predominance of optimal habitats (more than 60% forest cover), while values 2–3 individuals/100 km^2 and less are observed in areas which include a high proportion of agricultural lands and settlements with low forest cover [Belotti *et al.* 2015; Bluzma 2003; Jedrzejewski *et al.* 1996; Kozlo 2003; Sidorovich 2006].

Since the CEZ has a high percentage of the forest cover (63%, and on-going reforestation of former meadows), the local conditions appear to be optimal for lynx. We would therefore expect a density in excess of 1.0 individual/100 km^2.

Also favourable is a very low level of human disturbance and absence of persecution of lynx by people (Fig. 6). We estimate that, during the period of this study, the average density of people working in the CEZ does not exceed 1–2 persons/km^2. Most are concentrated in just a few areas (mainly Chornobyl town and the central technical area around the ChNPP) which occupy no more than 10–15% the total CEZ area. For the majority of the CEZ, the density of people is unlikely to exceed 0.1 person/km^2. Forestry activity is minimal and agricultural activity is virtually absent.

Finally, the CEZ is a rich source of food for lynx; they prefer relatively small sized ungulates: roe deer (*Capreolus capreolus*), and female and immature red deer (*Cervus elaphus*) [Belotti *et al.* 2015; Jedrzejewski *et al.* 1993; Mayer *et al.* 2012; Okarma *et al.* 1997; Schmidt 2008]. If present in high abundance, these two species have been reported to amount to 60–90% of the lynx diet (Table 4). Unfortunately, there have been no censuses of the ungulates in the Ukrainian CEZ. However, there are data for the adjoining Polessky State Radioecological Reserve (PSRER) of Belarus [Kuchmel 2008; Deryabina *et al.* 2015]. Since the natural conditions are similar in the Ukrainian CEZ to those in the PSRER, it is possible to assume that populations of the ungulates are of a similar order of magnitude and have developed similarly over time since the Chornobyl accident.

Fig. 6. Lynx often visit abandoned settlements in the CEZ: *a*, male p0443-1 is scent making a corner of the abandoned farm; *b*, adult lynx (no ID) is crossing an abandoned village (p0282), 25.01.2015; *c*, adult lynx (no ID) near the entrance to the abandoned farm (p0431), 23.02.2018.

Рис. 6. Рисі часто відвідують нежилі населені пункти ЧЗВ: *a* — самець p0443-1 робить сечову мітку у кинутій фермі; *b* — доросла рись (без ID) пересікає нежиле село (p0282), 25.01.2015; *c* — доросла рись (без ID) біля входу до кинутої ферми (p0431), 23.02.2018.

In the early 2000s, the density of roe deer in the PSRER reached 55–82 individuals/100 km^2, and red deer ca. 10 individuals/100 km^2 [Kuchmel 2008]; similar values were reported in 2005–2010 [Fig. S2: Deryabina *et al.* 2015] (Table 5). The density of ungulates in PSRER is 4–50 times less than the density of the ungulates in the Bialowieza Forest National Park (Poland) [Okarma *et al.* 1997] whose natural complexes are similar to those in the PSRER and CEZ. However, these data are already outdated; the population of red deer in the CEZ appears to be higher than that previously reported in the PSRER [Gashchak *et al.* 2006]. A comparatively high density of these prey species is also supported by our studies using camera traps in 2001–2005 [Gashchak 2008] and 2014–2016 [project TREE unpublished data] (Table 5).

Table 4. Diet composition of lynx in some regions of Europe, %

Таблиця 4. Склад раціону рисі у деяких регіонах Європи, %

Region	Roe deer	Red deer	Hare	Reference
Bohemian Forest (Czech)	75.1–96.7[a] *62/58[b]	3.3–24.9[a] *11/2[b]	2.2[a] *9/4[b]	[a] Belotti et al. 2015 [b] Mayer et al. 2012
Bialowieza Forest (Poland)	**81–86[c] 62[d]	– 22[d]	11–29c 9d	[c] Jedrzejewski et al. 1993 [d] Okarma et al. 1997
Vitebsk region (Belarus)	4.3–-35.7[e] 10.2–32.5[f]	0.6-8.4[e] –	48.4–82.5[e] 37–52[f]	[e] Kozlo 2003 [f] Sidorovich 2006

*Winter/summer data; **Roe and red deer in total.

Table 5. Density of lynx and its main prey in different regions of Europe, individuals/100 km^2 (superscript letter identifies reference)

Таблиця 5. Щільність рисі і її головних жертв у різних регіонах Європи, особин/100 км^2 (надстроковий індекс вказує на джерело інформації)

Region	Roe deer	Red deer	Hare*	Lynx*	Reference
Density, individuals/100 km^2					
Bohemian Forest (Czechia)	161[b]	156[b]	(500–1700)[a] (1900–2500)[c]	0.4–0.9[d]	[a] Cukor *et al.* 2018 [b] Belotti *et al.* 2015 [c] Smith *et al.* 2005 [d] Weingarth *et al.* 2012
Bialowieza Forest (Poland)	**382/635[g]	**461/653[g]	(280–610)[e] (410–950)[f]	2.4–3.2[g]	[e] Husek *et al.* 2021 [f] Kamieniarz *et al.* 2013 [g] Okarma *et al.* 1997
Vitebsk region (Belarus)	20–80[h]	5–15[h]	250[h]	1.8–4.3[i]	[h] Kozlo 2003 [i] Sidorovich 2006
Polessky State Radioecological Reserve (Belarus)	55–82[m,k]	10–12[m,k]	36–54[m]; (200–400)[n]	1.4–1.9[j;] (0.1–1.6)[l]	[j] Deriabina 2008 [k] Deryabina *et al.* 2015**** [l] Kozlo 2003 [m] Kuchmel 2008 [n] Savitsky *et al.* 2005
Frequency of records by camera traps, individuals/100 TD					
CEZ (Ukraine): 2001–2005***	3.0	1.1	0.9	0	Gashchak 2008
CEZ (Ukraine): 2014–2016	4.2	16.2	5.9	0.4	TREE project unpublished data (provisional estimates)

* In brackets—data for vaster surrounding region, not for the particular one; ** Winter/summer data; *** We think the camera traps used in 2001–2005 (Yashica T4D, Forestry Suppliers, Inc. Wildlife Pro Camera) missed a lot of animals since it had 20-sec delay between consecutive triggerings and likely missed animals in larger groups, and therefore these values are considered underestimates; **** Values recalculated from Figure S2, Supplemental information [Deryabina *et al.* 2015].

Our data for roe deer in 2001–2005 suggest 3.0 individuals/100 TD, and for red deer—1.1 individuals/100 TD [Gashchak 2008]. This is likely an underestimation as the camera traps (Yashica T4D, Forestry Suppliers, Inc. Wildlife Pro Camera) used 20-sec delay between triggerings and likely missed some animals in larger groups; the average number of individuals per event was 1.0. In 2014–2016 when we used camera traps with minimal delay between triggerings where we observed 1.25 and 1.98 individuals/event for roe deer and red deer respectively [TREE project provisional unpublished data]. If the latter values are used as a correction factor, then the frequency of records of roe deer and red deer in 2001–2005 could be closer to values of 3.0 × 1.25 = 3.75 ind./100 TD and 1.1 × 1.98 = 2.18 ind./100 TD respectively. If the frequency of records of roe deer in the CEZ corresponded to the density of the species reported in PSRER (55–82 individuals/100 km^2) [Kuchmel 2008], then density of red deer in the CEZ in 2001–2005 would approximate to 55 × (2.18/3.75) … 82 × (2.18/3.75) or 32–48 individuals/100 km^2.

Regular visual observations in the subsequent 10-year period allow us to suggest that red deer have gradually become the most abundant ungulate in the CEZ. If we assume that data on the recording frequency more or less correlate with the density of ungulates [Rowcliffe *et al.* 2008], then in 2014–2016 (Table 5) the density of roe deer and red deer could be near (55÷88) × (4.2/3.75) = 208÷311 and (32÷48) × (16.2/2.18) = 238÷357 individuals/100 km^2 respectively. Even taking into account the approximate nature of such calculations, it suggests about the same order of density of roe deer and red deer as in Bialowieza Forest (Poland) (Table 5) which supports a density of lynx 2–3 individuals/100 km^2 [Okarma *et al.* 1997].

Among the other ungulates inhabiting the CEZ (wild boar *Sus scrofa*, Eurasian elk *Alces alces*, Przewalski horse *Equus ferus*, European bison *Bison bonasus*), lynx can only take wild boar and potentially young elk. The importance of the boar in the diet of lynx has been reported to be low in Bialowieza Forest (Poland) amounting to only 2–3% of intake, reaching 11% when there is a low abundancy of roe deer and high abundancy of wild boar [Jedrzejewski *et al.* 1993; Okarma *et al.* 1997; Schmidt 2008].

In the more northern regions of Europe, the main component of the lynx's diet is hare (brown hare *Lepus europaeus* and mountain hare *Lepus timidis*) [Jedrzejewski *et al.* 1993; Kozlo 2003; Sidorovich 2006]. However, they are considered as a reserve food source compensating for a lack of ungulates. Moreover, it is considered that lynx can reach high number only when there is an abundance of ungulates [Sidorovich 2006]. As ungulate population sizes grow, the lynx's home range decreases, and overlap of individual home ranges becomes more common [Jedrzejewski *et al.* 1993; Schmidt 2008]. Hare numbers in the CEZ are relatively low with brown hare being the predominant species [Gashchak *et al.* 2006]; mountain hare are rare [Gashchak 2018]. The recorded frequency of brown hare by the camera traps in 2001–2005 was 0.9 individuals/100 TD [Gashchak 2008] (see discussion above regarding the likely underestimation in this study). In 2014–2016, it was 5.9 individuals/100 TD [TREE project provisional unpublished data]. Summary density of two species in the PSRER in the early 2000s was estimated as 36–54 individuals/100 km^2 [Kuchmel 2008] which is an order of magnitude lower than in some other regions of Europe with lynx; 250–2500 individuals/100 km^2 have been recorded at some sites in Poland and Belarus [Cukor *et al.* 2018; Husek *et al.* 2021; Kamieniarz *et al.* 2013; Kozlo 2003; Smith *et al.* 2005]. This is consistent with both the PSRER and the CEZ being mainly woodlands with no agricultural lands; the highest densities of the hare are observed in mosaic agricultural habitats and decrease as the amount of woodland increases [Smith *et al.* 2005]. From our data 2014–2016 [TREE project provisional unpublished data], the recorded frequency of hare inside the forest sites amounted to 4.5 individuals/100 TD, whilst on the forest edge and in former meadows it was 6.7–9.3 individuals/100 TD. Hare are therefore likely to play a secondary role in the diet of lynx.

The relatively high density of ungulates, the extent of forest cover and the absence of persecution and disturbance by people mean that the CEZ should be a good habitat for lynx with potentially high densities of the species being expected. Our trap camera footage does not give direct assessment of lynx numbers since the various studies did not cover the whole of the CEZ territory and data were obtained over different years from different sites. The pattern of CT deployment within the study sites and duration of CT deployment also differed from the project to project. However, we consider that it is possible to combine these data and consider them representative of sub-populations of lynx in the CEZ. In attempting to analyse our data we considered:

1) Lynx were regularly recorded at the all of our study sites, regardless of the size of the site, its position within the CEZ and the number of CTs used. The size of our study sites (20–175 km^2) was comparable with known home range areas for lynx (40–250 km^2, 3.6–8.9 km radius) [Filla *et al.* 2017; Belotti *et al.* 2015; Jedrzejewski *et al.* 1996; Matyushkin & Vaisfeld 2003; Schmidt 1998]. From our studies, which covered a total of 811 km^2 across the CEZ (2600 km^2), we think it is reasonable to assume that lynx inhabit all of the CEZ.

2) Based on the size of our study sites, the known home range of lynx and the distance between our study sites (3 to 40 km) we consider that it is reasonable to anticipate that most immature individuals and individual adult females would be recorded at 1–3 study sites. Some adult males could visit study sites over a more broad territory (including crossing over the Prypiat river) since their home ranges are larger (90–250 km^2). If an individual was recorded several times within a study site then we can assume that the site, at the least partially, includes the home range of that animal.

3) Since the CEZ is characterised by relatively high ungulate numbers with forests being the dominant habitat, the individual home ranges of lynx could be relatively small, and the overlapping of the home range of several individuals could be possible. For the same reasons we assumed that most individuals would exhibit home range fidelity during the 5–6 years of our observations. Dispersion of immature animals from the maternal home range could be in any direction.

4) The intrusion of individuals from remote territories is possible (during the mating season (February–March) and dispersion of immature animals); this is equally probable in any direction. Some individuals will never leave their home range.

5) Passage of lynx between Ukraine (CEZ) and Belarus (PSRER) is likely to occur in both directions; the conditions of both territories (abundance of prey, forest cover, protected status, few people) are similar. Therefore, the influence of transboundary movement on the estimation of lynx numbers within the Ukrainian CEZ could be considered to be minimal.

6) Movement between the CEZ and surrounding agricultural and forestry lands to the south and west is possible. However, the presence of people and regular economic activities outside of the CEZ make conditions there less favourable for lynx (less ungulates, lower forest cover, higher disturbance, possible persecution). These areas are unlikely to provide new individuals into the CEZ and there is likely to be negligible outflow. Therefore, the migration of lynx to/from the west and south can be ignored when trying to establish lynx numbers in the CEZ.

7) Lynx generally move comparatively slowly (1–1.5 km/h) travelling in irregular directions for typically 6 to 7 hours per day (rarely up to 12 hours) [Jedrzejewski *et al.* 2002; Schmidt 1999; Podolski *et al.* 2013]. The probability of recording a lynx at a specific CT location is relatively low. The probability of recording males increases in the mating season (February–March), whilst recording of females may be higher when they are nursing small cubs [Heptner & Naumov 1972; Naidenko 2019; Schmidt 1999; Jedrzejewski *et al.* 2002]. However, since only 75% of adult females breed [Jedrzejewski *et al.* 2002], and, during the mating period, lynx normally concentrate at a few sites [Heptner & Naumov 1972], there is a decreased probability of recording lynx over the rest of the territory (Fig. 7).

8) The natural yearly mortality of lynx (older than 1 year) is reported to be 5–10% [Jedrzejewski *et al.*, 1996; LIFE Lynx https://www.lifelynx.eu/biology/]. Since poaching in the CEZ is likely minimal, it is possible to assume that most of the lynx population survived the 5–6 years of our studies. If the animals had home range fidelity and this fidelity lasted over the 5–6 years of our studies, and the yearly mortality was 5–10%, then our data can be interpreted to give an estimate of the size of lynx population within the Ukrainian CEZ.

Among the 302 records of the lynx we could identify individuals in 125 cases; from these we could identify 50 individual animals. Whilst identified individuals could also be among the unidentified animals (e.g. because of poor picture quality), it is also likely that photographs of unidentified individuals record additional individuals. Consequently, the total number of lynx in our study areas could be more than 50. Our total study area amounted to only 811 km^2, or about 30% total area of the CEZ. The presence of additional lynx in the rest of the CEZ (i.e. nearly 70% of the total area) is probable.

The area of our study sites (20–175 km^2; 2.5–7.4 km radius) and the size of the lynx home range (40–250 km^2; 3.6–8.9 km radius) [Filla *et al.* 2017; Belotti *et al.* 2015; Jedrzejewski *et al.* 1996; Matyushkin & Vaisfeld 2003; Schmidt 1998] are broadly comparable. The CTs operated for no more than a year (often only a few months) at a given location before being moved to a new location within the study site (typically for the TREE project 1–3 km distant) or to new site between 5–20 km away. Half of the identified animals (26 of 50) were recorded only once. This may mean that the animals were migrants (i.e. not resident in the locality of the camera trap) or it may simply be because the animals did not visit other sites with CTs. However, as already noted it is also possible that identified individuals were recorded on those photographs from which individual identification was not possible.

Among those animals recorded two or more times only four of 26 individuals were recaptured over 10–23 km from the location of a previous record (see: Table 2). The rest were repeatedly recorded at the same site (maximum distance 3.5 km between outermost locations); this included those lynx recorded many times over two years (e.g. IDs p0137-1 and p0273-1, see: Table 2). Data for the repeat captured lynx suggest that these individuals were keeping to their own home range, and that potentially their home range was not large.

We do not know if we are capturing images of migrating/nomadic individuals, which come into the CEZ from the remote areas. However, including all observations within our analyses is justifiable; migrating/nomadic animals contribute to the development of the local population and functioning of the ‘predator–prey’ system. It is likely that some migrating/nomadic animals are always present in the CEZ. We assume that the identified individuals are the main inhabitants of the sites surveyed within the CEZ and that among the unidentified animals some of them will be migrants.

If we use only the identified animals, the resultant estimate of the density of lynx for the study sites will likely be an underestimate as we are ignoring the unidentified animals which could include additional individuals. Estimated density based only on identified individuals are presented in the Table 6.

The density of lynx vary over a relatively large range (0 to 13.1 individuals/100 km^2). Analysis of the images demonstrates that high values are normally associated with family groups and/or the mating period.

Fig 7. Mating ritual, four lynx total during the event: female p0166-1 (left), male p0167-1 (centre), one cub of the female p0166-1 (right), the second cub—out of the frame, 13.03.2014.

Рис. 7. Шлюбний ритуал рисі, всього чотири звіра під час події: самиця p0166-1 (зліва), самець p0167-1 (у центрі), одне дитинча самиці p0166-1 (справа), друге дитинча – поза кадром, 13.03.2014.

Table 6. Density of lynx estimated from the identified individuals (D_{ID}) and frequency of lynx records (FR_{ID}—only identified individuals, FR_{all}—all records) at study sites in 2013–2018; mean (SD). The order follows the frequency of all records (FR_{all})

Таблиця 6. Щільність рисі оцінена по індивідуально визначеним особинам (D_{ID}) і частота реєстрації рисі (FR_{ID} — тільки ідентифіковані особини, FR_{all} — всі випадки реєстрації) на дослідних ділянках у 2013–2018; середнє значення (стандартне відхилення). Загальний порядок розташування рядків відповідає зростанню значень FR_{all}

Year	Site	D_{ID}	FR_{ID}	FR_{all}	FR_{all}/FR_{ID}
		individuals/100 km^2	individuals/100 TD	individuals/100 TD	
2018	1	0, n_{ID} = 0	0, n_p = 1	0, n_p = 1	-
2018	3	0.6, n_{ID} = 1	0.05 (0.14), n_p = 9	0.05 (0.14), n_p = 9	1.00
2016	3	0, n_{ID} = 0	0 (0), n_p = 22	0.13 (0.43), n_p = 22	-
2017	5	1.7, n_{ID} = 2	0.05 (0.19), n_p = 25	0.19 (0.52), n_p = 25	3.53
2014	1	0, n_{ID} = 0	0 (0), n_p = 13	0.19 (0.70), n_p = 13	-
2015	1	0.8, n_{ID} = 1	0.02 (0.18), n_p = 95	0.23 (1.29), n_p = 95	12.77
2016	2	4.1, n_{ID} = 7*	0.09 (0.30), n_p = 37	0.28 (0.59), n_p = 37	2.95
2018	5	2.6, n_{ID} = 3	0.08 (0.16), n_p = 14	0.34 (0.59), n_p = 14	4.19
2016	5	1.7, n_{ID} = 2	0.09 (0.39), n_p = 19	0.36 (0.66), n_p = 19	4.00
2018	8	8.4, n_{ID} = 2	0.23 (0.36), n_p = 7	0.37 (0.57), n_p = 7	1.60
2015	3	1.7, n_{ID} = 3	0.09 (0.58), n_p = 95	0.37 (0.94), n_p = 95	4.05
2016	1	0.8, n_{ID} = 1	0.31 (1.53), n_p = 24	0.39 (1.56), n_p = 24	1.26
2017	2	0.6, n_{ID} = 1	0.43, n_p = 1	0.43, n_p = 1	1.00
2015	7	0, n_{ID} = 0	0 (0), n_p = 3	0.48 (0.82), n_p = 3	–
2015	2	4.7, n_{ID} = 8*	0.24 (0.88), n_p = 99	0.57 (1.25), n_p = 99	2.39
2018	4	0, n_{ID} = 0	0 (0), n_p = 3	0.62 (0.25), n_p = 3	–
2017	8	4.2, n_{ID} = 1	0.38 (1.01), n_p = 7	0.65 (1.13), n_p = 7	1.70
2013	2	1.2, n_{ID} = 2*	0.49 (0.69), n_p = 2	0.73 (1.03), n_p = 2	1.50
2018	6	7.9, n_{ID} = 7*	0.43 (0.90), n_p = 14	0.74 (1.10), n_p = 14	1.74
2014	3	0.6, n_{ID} = 1	0.64 (1.86), n_p = 14	0.81 (1.90), n_p = 14	1.26
2018	2	0.6, n_{ID} = 1	0.08 (0.18), n_p = 5	0.88 (0.90), n_p = 5	10.67
2014	2	2.4, n_{ID} = 4*	0.50 (1.58), n_p = 24	0.99 (1.90), n_p = 24	1.99
2016	7	0, n_{ID} = 0	0 (0), n_p = 3	1.04 (1.26), n_p = 3	–
2015	5	2.6, n_{ID} = 3	1.04 (1.47), n_p = 2	1.56 (2.20), n_p = 2	1.50
2014	5	0.9, n_{ID} = 1	0.62, n_p = 1	2.49, n_p = 1	4.00
2013	4	9.4, n_{ID} = 5*	1.54 (1.61), n_p = 5	2.60 (1.62), n_p = 5	1.69
2014	4	13.1, n_{ID} = 7**	4.24 (3.90), n_p = 5	8.60 (7.25), n_p = 5	2.03
Total		2.6 (3.3), n_{YS} = 27	0.21 (0.93), n_P = 549	0.51 (1.52), n_P = 549	3.16 (3.06), n = 21

Note: n_{ID}—number of the identified individual lynx, n_{YS}—number of 'year-site' pairings; n_p—number of locations with a CT;, *one family group observed; **two family groups observed. Total D_{ID}—average of D_{ID} in the column; total FR_{ID} and FR_{all}—average of values for site/year means (n = 549), see Methods above; Total FR_{all}/FR_{ID}—average of all FR_{all}/FR_{ID} values in the column.

Despite the approximate nature of our estimations the density of lynx correspond to ranges observed in other parts of Europe: up to 5–10 individuals/100 km^2 in optimal habitats, including in north Belarus, Lithuania, and the Bialowieza Forest (Poland) [Jedrzejewski *et al.* 1996; Bluzma 2003; Kozlo 2003; Sidorovich 2006]. In sub-optimal habitats 0.4–1.0 individuals/100 km^2 have been recorded [Matyushkin & Vaisfeld 2003; Belotti *et al.* 2015].

Rowcliffe *et al.* [2008] argued that records obtained by the CTs should only be used to calculate the density of the animals if the population is closed. In the case of lynx in the CEZ the population is open. The frequency of records (individuals/100 TD) could be used either as an index of relative abundance and/or as an indication that additional individuals are present at a site. Values of FR_{all} on average exceeded FR_{ID} by more than three times (see: Table 6). The higher value of FR_{all} could be because images are of known animals but the image quality was such that the animal could not be identified and also that images contain additional unidentified individuals. In the first case it is reasonable to anticipate positive correlation FR_{delta} ($FR_{delta} = FR_{all}–FR_{ID}$) and FR_{ID}. Unrecognised additional individuals would likely result in no relationship between FR_{delta} and $FR_{ID.}$ Our FR_{delta} data show some relationship between FR_{ID} ($R^2 = 0.34$, $p = 0.008$, Fig. 8) and FR_{delta}. Whilst the potential for some additional unknown individuals cannot be excluded, their contribution is unlikely to be.

Such a relationship may suggest a dependence of FR_{delta} on the number of the identified animals (n_{ID}). However no correlation was found ($R^2 = 0.07$, $p = 0.26$) between these parameters, likely this was because of the varying density of CTs in our study (one CT per ca. 3–240 km^2).

If the average density is 2.6 ind./100 km^2 (see: Table 6), then up to 21 individuals should inhabit the total area of our study sites (811 km^2); this value is less than the number of identified individuals we observed (n = 50, see: Table 2). However, it is likely that the total home range of the identified lynx is larger than 811 km^2. If the density of lynx is relatively consistent across the CEZ then 50 individuals could be expected to inhabit a total area of about 1920 km^2. Consequently, up to 68 lynx could be on the total territory of Ukrainian CEZ (2600 km^2).

Although our study sites occupy about 30% total area of the CEZ area, they do not represent all the ecological conditions/habitats of the CEZ. Habitats are a mosaic of forest and former meadow lands; the forests are of different ages and species composition and the former meadows are actively being colonised by trees and shrubs. The area has a large network of drainage channels, areas of reed beds and river floodplain. In the north-west, south and east of the CEZ, over approximately 1000 km^2 where we had few CTs sited the forests are largely a monoculture of pine plantations (predominantly *Pynus sylvestris*) with poor undergrowth.

Large areas in the central part of the CEZ are relatively dry former agricultural land with pine and birch reforestation and again we had few CTs in these habitats; there are few data relating to lynx from such habitats. If lynx abundance depends on the prey abundance, and the later in turn depends upon the richness of plant forage, it is likely that there could be a lower density of lynx in the habitats in these unstudied areas.

The lowest estimations of the lynx in Europe range from 0.4 to 1.0 individuals/100 km^2 [Belotti *et al.* 2015; Matyushkin & Vaisfeld 2003]. In order to avoid overestimation we assumed 3–7 lynx represent the population of the remaining unstudied territories (680 km^2). Therefore, we suggest that at least 53–57 lynx could live in the CEZ territory.

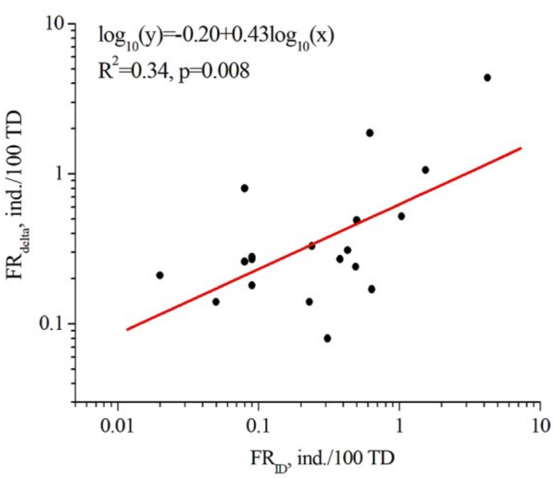

Fig. 8. Relationship between the difference ($FR_{delta} = FR_{all}–FR_{ID}$) on the frequency of records of identified individuals (FR_{ID}).

Рис. 8. Залежність різниці між частотою реєстрації всіх і лише ідентифікованих особин ($FR_{delta} = FR_{all}–FR_{ID}$) і частоти реєстрації ідентифікованих особин (FR_{ID}).

Our estimates (ca. 53–57 (potentially up to 68) individuals) are based on the data from studies which were not designed for this purpose. In the Belarussian part of the exclusion zone up to 40 lynx were recorded in the mid-2000s [Deryabina 2008]; compared to these data our estimates seem reasonable. Large-scale, long-term lynx-oriented studies are necessary to provide better estimates for the CEZ region. However, it is currently reasonable to state that the CEZ has become important for the Eurasian lynx in Polissia region and plays a significant role in its recovery in this part of Europe. The CEZ Eurasian lynx local population has become one of the most densely populated in Ukraine [Shkvyria & Shevchenko 2009; Zhyla 2021]. Establishment, in 1986, of a *de facto* reservation of 2600 km^2 in Ukraine and 2170 km^2 in adjoining Belarus has created favourable conditions for lynx recovery and demonstrates the conservation benefits that even unmanaged rewilding can achieve.

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References

Barnett, C. L., S. Gashchak, C. Wells, E. Guliaichenko, M. D. Wood, N. A. Beresford. 2022. Motion-activated camera trap images of wildlife from the Red Forest, Chornobyl, Ukraine, 2016–2017. *NERC EDS Environmental Information Data Centre*, [Dataset].

Belotti, E., N. Weder, L. Bufka, A. Kaldhusdal, H. Küchenhoff, [et al.] 2015. Patterns of Lynx predation at the interface between protected areas and multi-use landscapes in Central Europe. *PLoS ONE* **10** (9): e0138139. CrossRef

Beresford, N. A., C. L. Barnett, S. Gashchak, V. Kashparov, S. Kireev, [*et al.*]. 2021. Wildfires in the Chernobyl Exclusion Zone – risks, consequences and management. *Integrated Environmental Assessment and Management,* **17** (6): 1141–1150. CrossRef

Bluzma, P. 2003. Lynx of Eurasia: Lithuania. *In:* Ye. Matyushkin, M. Vaisfeld (eds). *The Lynx. Regional Features of Ecology, Use and Protection.* Nauka, Moscow, 105–117. [In Russian]

Deryabina, T. G. 2008. Distribution and number of the large mammals (bison, bear, lynx, badger) included into the Red Book of Belarus Republic in the territory of Paliessie State Radiation and Ecology Reserve. *In:* G. V. Antsipov (ed.) *Faunal studies in Paliessie State Radiation and Ecology Reserve*. Institute of Radiology, Homel, 19–35. [In Russian]

Deryabina, T. G., S. V. Kuchmel, L. L. Nagorskaya, T. G. Hinton, J. C. Beasley, [et al.]. 2015. Long-term census data reveal abundant wildlife populations at Chernobyl. *Current Biology*, **25**: R811–R826. CrossRef

Filla, M., J. Premier, N. Magg, C. Dupke, I. Khorozyan, [et al.]. 2017. Habitat selection by Eurasian lynx (Lynx lynx) is primarily driven by avoidance of human activity during day and prey availability during night. *Ecology and Evolution,* **7** (16): 6367–6381. CrossRef

Gaschak, S. P. 2008. About an experience of automatic photography of wild animals in Chornobyl zone. *In:* Zagorodniuk, I. (ed.). *Rare Theriofauna and Its Conservation*. Luhansk, 28–36. (Series: Proceedings of the Theriological School; Vol. 9). [In Ukrainian]

Gashchak, S. P., Y. O. Gulyaichenko, N. A. Beresford, M. D. Wood. 2016. Brown bear (Ursus arctos L.) in Chernobyl exclusion zone. *Proceedings of Theriological School,* **14:** 71–84. CrossRef

Gashchak, S. P., Y. O. Gulyaichenko, N. A. Beresford, M. D. Wood. 2017. European bison (Bison bonasus) in the Chornobyl exclusion zone (Ukraine) and prospects for its revival. *Proceedings of Theriological School*, **15**: 58–66. CrossRef

Gashchak, S. P. 2018. Vertebrates of Chornobyl zone (Chornobyl radiation and ecological biosphere reserve) included into Red list of Ukraine (2009). *In: Problems of the Chornobyl exclusion zone*. Slavutych, **18**: 5–54. [In Russian]

Gashchak, S., S. Paskevich. 2019. Przewalski's horse (Equus ferus przewalskii, Poljakov, 1881) in Chornobyl exclusion zone 20 years after introduction: number, population structure and distribution. *Theriologia Ukrainica*, **19**: 80–100. CrossRef

Gashchak, S. P., D. O. Vyshnevsky, O. O. Zalisky. 2006. *Vertebrate Fauna of the Chornobyl Exclusion Zone (Ukraine)*. Publishing House of ChTsPYaBRVR, Slavutych, 1–100. [In Ukrainian]

Gashchak, S., S. Paskevych, E. Gulyaichenko, D. Vyshnevskyi, C. L. Barnett, N. A. Beresford. 2022. Motion-activated camera trap images of Eurasian Lynx in the Ukrainian Chornobyl Exclusion Zone, 2013–2018. *NERC EDS Environmental Information Data Centre* [Dataset] CrossRef

Duľa, M., M. Bojda, D. B. H. Chabanne, P. Drengubiak, H. Ľuboslav, [et al.]. 2021. Multi-seasonal systematic camera-trapping reveals fluctuating densities and high turnover rates of Carpathian lynx on the western edge of its native range. *Scientific Reports*, **11**: 9236. CrossRef

Heptner, V. G., N. P. Naumov. 1972. *Mammals of the Soviet Union. Volume 2, Issue 2. Carnivores (Hyenas and Cats)*. Vysshaia Shkola, Moscow, 1–552. [In Russian]

Jedrzejewski, W., B. Jedrzejewska, H. Okarma, K. Schmidt, A. N. Bunevich, L. Milkowsky. 1996. Population dynamics (1869–1994), demography, and home ranges of the lynx in Bialowieza Primeval Forest (Poland and Belarus). *Ecography*, **19** (2): 122–138. CrossRef

Jêdrzejewski, W., K. Schmidt, L. Milkowsky, B. Jêdrzejewska, H. Okarma. 1993. Foraging by lynx and its role in ungulate mortality: the local (Bialowieza Forest) and the Palaearctic viewpoints. *Acta Theriologica*, **38** (4): 385–403. CrossRef

Jedrzejewski, W., K. Schmidt, H. Okarma, R. Kowalczyk.

2002. Movement pattern and home range use by the Eurasian lynx in Bialowieza Primeval Forest (Poland). *Annales Zoologici Fennici*, **39**: 29–41.

Kirikov, S. V. 1960. *Changes of Fauna in Natural Areas of the USSR (in the 13th–19th centuries). Forestlands and Forest Tundra.* Publishing House of the USSR Academy of Sciences, Moscow, 1–158. [In Russian]

Kozlo, P. G. 2003. Lynx of Eurasia: Byelorussia. *In:* Ye. Matyushkin, M. Vaisfeld (eds). *The Lynx. Regional Features of Ecology, Use and Protection.* Nauka, Moscow, 118–137. [In Russian]

Kuchmel, S. V. 2008. Species composition of mammals of Orders Insectivora, Lagomorphs, Carnivorans, Rodents and Odd-toed Ungulate in Paliessie State Radiation and Ecology Reserve. *In:* G. V. Antsipov (Ed.) *Faunal studies in Paliessie State Radiation and Ecology Reserve*. RNIUP Institute of Radiology, Homel, 38–64. [In Russian]

LIFE Lynx. Project (LIFE16 NAT/SI/000634, 01/07/2017 – 31/03/2024): Preventing the Extinction of the Dinaric-SE Alpine Lynx Population Through Reinforcement and Long-term Conservation. https://www.lifelynx.eu/biology/

Matyushkin, Ye. N., M. A. Vaisfeld. 2003. *The Lynx. Regional Features of Ecology, Use and Protection*. Nauka, Moscow, 1–523. [In Russian]

Mayer, K., E. Belotti, L. Bufka, M. Heurich. 2012. Dietary patterns of the Eurasian lynx (Lynx lynx) in the Bohemian forest. *Saugetierkundliche Informationen*, **8** (45): 447–453.

Naidenko, S.V. 2019. *Reproduction Biology of Felids: Mechanisms for Increase of the Reproduction Success*. Association of scientific issues KMK, Moscow, 1–192. [In Russian]

Marynych, A. M. *et al.* (eds). 1985. *Nature of Ukrainian SSR. Landscapes and Physical-Geographical Zoning.* Naukova Dumka, Kyiv, 1–224. [In Russian]

Okarma, H., W. Jêdrzejewski, K. Schmidt, R. Kowalczyk, B. Jêdrzejewska. 1997. Predation of Eurasian lynx on roe deer and red deer in Bialowieza Primeval Forest, Poland. *Acta Theriologica*, **42** (2): 203–224. CrossRef

Podolski, I., E. Belotti, L. Bufka, H. Reulen, M. Heurich. 2013. Seasonal and daily activity patterns of free-living Eurasian lynx Lynx lynx in relation to availability of kills. *Wildlife Biology*, **19** (1): 69–77. CrossRef

Rowcliffe, J. M., J. Field, S. T. Turvey, C. Carbone. 2008. Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology*, **45**: 1228–1236. CrossRef

Savitsky, B. P., S. V. Kuchmel, L. D. Burko. 2005. *Mammals of Belarus*. (Ed.) Savitsky, B. P. Publishing Center of Belarus State University, Minsk, 1–319. [In Russian]

Sidorovich, V. E. 2006. Relationship between prey availability and population dynamics of the Eurasian lynx and its diet in northern Belarus. *Acta Theriologica*, **51**: 265–274. CrossRef

Shkvyria, M. G., L. S. Shevchenko. 2009. Lynx. Lynx lynx. *In:* I. A. Akimov (Ed.) *The Red Data Book of Ukraine. Animals*. Hlobalkonsaltynh, Kyiv, 546. [In Ukrainian]

Schmidt, K. 1998. Maternal behaviour and juvenile dispersal in the Eurasian lynx. *Acta Theriologica*, **43**: 391–408. CrossRef

Schmidt, K. 2008. Behavioural and spatial adaptation of the Eurasian lynx to a decline in prey availability. *Acta Theriologica*, **53**: 1–16. CrossRef

Smith, R. K., N. V. Jennings, S. Harris. 2005. A quantitative analysis of the abundance and demography of European hares Lepus europaeus in relation to habitat type, intensity of agriculture and climate. *Mammal Review*, **35** (1): 1–24. CrossRef

Sokur, I. T. 1961. *Historical Changes and Use of Mammals Fauna in Ukraine*. AS Ukr. SSR, Kyiv, 1–84. [In Ukrainian]

Weingarth, K., C. Heibl, F. Knauer, F. Zimmermann, L. Bufka, M. Heurich. 2012. First estimation of Eurasian lynx (Lynx lynx) abundance and density using digital cameras and capture–recapture techniques in a German national park. *Animal Biodiversity and Conservation*, **35** (2): 197–207. CrossRef

Wood, M. D., N. A. Beresford. 2016. The wildlife of Chernobyl: 30 years without man. *The Biologist*, **63** (2): 16–19. https://t.co/0IKjXLcif3

Zhyla, S. M. 2002. Bobcat in the Ukrainian Polissia: Population status and distribution. *Visnyk of Lviv University. Biology*, **30**: 61–64. [In Ukrainian]

Zimmermann, F., C. Breitenmoser-Wursten, U. Breitenmoser. 2007. Importance of dispersal for the expansion of a Eurasian lynx Lynx lynx population in a fragmented landscape. *Oryx*, **41** (3): 358–368. CrossRef