TITLE PAGE

Recolonisation dynamics of grey wolves: delayed recovery in a Central European country

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Author contribution statement

MK conceptualised the study and led the writing of the manuscript. AV, GC, BČB and PH elaborated on their respective sections according to their areas of expertise. AV, MD, MB, BČ, KC, LF, JH, KM, JM, AS and LŽ contributed substantially to the data collection. GC analysed population trends and growth rates, and prepared Figures 3–5. MK analysed population density and pack size development, preparing Figures 1, 2 and 6. AB, BČB, SC, JŠ, NT and PH analysed the genetic data. All authors contributed to the editing and review of the manuscript.

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Ethics approval statement

The trapping of live animals was authorised by local nature protection authorities and followed the ethical standards set by collaborating universities and governments, i.e., Czech University of Life Sciences: MZP/2018/630/2582, MZP/2022/630/929, SZ NPS 08816/2020/4, SZ SNPCS 00118/2022, KUUK/049576/2022; Mendel University in Brno: SR/0012/US/2021-5; MZP/2022/630/735; and the Government of Lower Austria: LF1-TVG-59/001-2018.

Abstract:
Grey wolves have been recovering throughout Europe over the last decades, widely portrayed as a conservation success story. We evaluated the trends and demography of two wolf populations that recolonised the Czech Republic between 2011/2012 and 2022/2023, integrating a variety of fieldwork and laboratory methods including snow tracking, camera trapping, telemetry and non-invasive genetics, with some of these methods being carried out within a citizen science framework. We then compared these demographic trends with the frequency of wolf attacks on livestock. Wolf territories grew annually by $\lambda = 1.25 \pm 0.18$ (0.92–1.68) in the Carpathian and $\lambda = 1.39 \pm 0.08$ (1.22–1.57) in the Central European population. Over the same period, the growth rate of wolf attacks on livestock exceeded the growth rate of territories. Wolf pack sizes averaged 5.7 ± 0.24 individuals in autumn and winter, but packs in their first and second year were significantly smaller than those occupying a territory for at least three years. The wolf density in areas occupied by a wolf pack reached, on average, 4.19 ± 0.49 individuals per 100 km^2. Overall, the recovery of the Central European wolf population in Czechia was delayed compared with neighbouring

Germany and western Poland, and the Carpathian population recovered even six years later. We discuss that this delayed recovery may have been influenced by hunting pressure in neighbouring Slovakia prior 2021 or by other undetected sources of mortality, making the population vulnerable in the long term.

MAIN TEXT

1. Introduction

Recovery of large carnivores, such as grey wolves (*Canis lupus*), represents both a remarkable conservation success and one of the most complex challenges in contemporary conservation biology. In recent decades, grey wolf populations have recovered substantially across Europe, driven by legal protection, increasing public awareness, land use changes, species adaptability and other factors (Chapron et al., 2014; Di Bernardi et al., 2025). This resurgence has sparked contentious debates, as wolves recolonise areas where they have long been absent, leading to conflicts with human activities such as livestock farming and hunting.

Rapid recolonisation has been documented especially in Central Europe: wolves from Eastern Europe immigrated in early 2000's to Western Poland and Germany (Nowak and Mysłajek, 2016; Reinhardt et al., 2019) and established a distinct population there (Szewczyk et al., 2021), initially named the Central European Lowland population (Chapron et al., 2014). This lowland population has since expanded its range up to Denmark, Belgium, the Netherlands, Austria and Czech Republic (Di Bernardi et al., 2025).

Among European large carnivores, wolves are the most adaptable species and are able to live in landscapes highly altered by humans (Chapron et al., 2014). Their expansion in Central Europe followed full legal protection of the species in Poland since 1998 (Mysłajek and Nowak, 2015). Wolves dispersed mostly in the northwestern and northeastern directions, including areas with high human population densities and intensively cultivated landscapes (e.g., in Lower Saxony, on average 190 people/km2, Ronnenberg et al., 2017). Nevertheless, the first recolonised areas in Germany were military training areas, likely due to reduced anthropogenic mortality (Reinhardt et al., 2019).

Despite the overall conservation success (Chapron et al., 2014; Di Bernardi et al., 2025), wolf-human interactions in human-dominated landscapes remain complex and the population growth has been limited in certain parts of Central Europe. For example, wolf mortality in the Jutland peninsula (Denmark and Schleswig-Holstein, Germany) was unsustainably high due to cryptic poaching (Sunde et al., 2021). The study indicated that the high rate of illegal killing was caused by the high rate of wolf-human encounters in an intensively cultivated and densely populated landscape. Furthermore, the number of wolves illegally killed in neighbouring Poland was estimated on average 16 times higher than the annual average number of wolves found shot in the period 2017-2020 (Nowak et al., 2021). Despite the overall positive trends at the European level, the results of these local studies suggest a continuously high anthropogenic impact on wolf population dynamics.

The wolf had been completely extirpated from most of the range of present-day Czech Republic by the 17th and 18th centuries, although the last wolf was shot in 1914 in the Western Carpathians (Anděra and Červený, 2009). The species returned to the eastern part of the Czech Republic (the Western Carpathians) in the mid-1990s, when 1-3 packs were reported (Anděra et al., 2004). However, these wolves were reportedly poached (Bartošová, 1998), and only sporadic occurrences were recorded in the following decade (Kutal et al., 2016). Regardless of the exponential growth of the Central European wolf population in neighbouring Germany and western Poland (Nowak and Mysłajek, 2016; Reinhardt et al., 2019), no permanent occurrence was recorded in the Czech Republic during the same period until 2013 (Flousek et al., 2014; Kutal et al., 2017). Moreover, sufficient habitat has been identified within the country (Romportl et al., 2017), along with connections to surrounding areas of recent wolf occurrence (Hulva et al., 2018).

The grey wolf has been legally protected under national law since 1993 (Bartošová, 2005) and is listed in Annexes II and V of the Habitats Directive (the species was listed in Annex IV prior to its downlisting in 2025). However, the species has also been legally hunted in neighbouring Slovakia for decades (Kutal et al., 2016; Kutal and Dula, 2020). Different management approaches – from strict protection in Germany, Poland, and Austria to legal hunting in Slovakia (Kutal et al., 2024) – raise questions about whether, and how, these differences are reflected in population dynamics. Furthermore, the current species distribution in the country is a subset of two populations spreading across Central Europe: Carpathian and Central European Lowland (*sensu* Chapron et al. 2014).

Wolf monitoring is not an easy task since their population density is low, individuals roam over large home ranges (Mattisson et al., 2013; Vorel et al., 2024) and their behaviour is elusive. This creates significant challenges in terms of the resources, such as man power, time, technology, and finances, necessary to estimate population sizes at regional or national levels and to meet requirements for reporting on the conservation status of species under the

EU Habitats Directive. At the same time, the recolonisation of wolves has stimulated the interest of the general public in reporting observations or signs of their presence (Ludolphy et al., 2025). If properly managed, data collection through citizen science initiatives represents an opportunity to generate robust scientific evidence and to help address conservation problems (McKinley et al., 2017), such as insufficient actionable data and public distrust of science (Skarlatidou et al., 2024).

This study aims to describe wolf recovery and demography in the Czech Republic by estimating the minimum number of wolf territories annually between 2011/2012 and 2022/2023. To achieve this, we combined methods commonly used for wolf monitoring in human-dominated landscapes, including citizen science. We report pack sizes, population density and known mortality, as well as differences in growth rates and colonisation patterns between the Central European lowland and Carpathian populations, the two main sources of expansion under contrasting management regimes: strict protection versus legal culling. Finally, we analysed wolf depredations on livestock—an indicator often cited in conservation debates—to document recovery trends in the Czech Republic. We compared population growth with depredation trends and discussed implications for the current compensation system.

2. Methods

2.1 Data collection and treatment

Wolf monitoring in the Czech Republic is based on a combination of particular methods, such as snow tracking, collection of non-invasive samples for genetic analyses, camera trapping, telemetry and public reports, in accordance with a national methodology for large carnivore monitoring (Černá et al., 2020). Field activities were primarily focused on mountain ranges and large protected areas along the borders with Slovakia, Poland, Germany and Austria, where a substantial proportion of suitable habitat for large carnivores has been identified (Romportl et al., 2010 Fig. 1, Figure S1.1). For each year from 2011/2012 to 2022/2023, the minimum number of wolf territories and individuals were determined, with the "wolf year" defined as spanning from May 1st to April 30th of the following year.

2.1.1 Snow tracking and collection of genetic samples

The fieldwork was carried out by experienced staff from the Carnivore Conservation Programme of Friends of the Earth Czech Republic, the Czech University of Life Sciences Prague, the Nature Conservation Agency of the Czech Republic, České Švýcarsko National Park, Šumava National Park, Krkonoše National Park and by trained volunteers from the Carnivore Tracking Project (www.carnivores.cz). The fieldwork followed the approach established in the Western Carpathians since 2002, where the presence of wolves and lynx has been monitored through snow tracking and searching for other signs of presence (Kutal et al., 2016). Footprints, tracks and other signs of presence were documented year-round and all non-invasive samples (scat, hair, urine, oestrus blood) were collected for further analysis. Snow tracking allowed the identification of a territory in 43.6% of cases. In addition, tissue samples were collected from dead wolves and saliva samples from dead livestock after wolf predation.

2.1.2 Camera traps

In most of the study areas (67.7% of territories), a network of opportunistically placed camera traps was established along the forest roads or near rendezvous sites, identified by simulated howling (Nowak et al., 2007). Forest roads and crossroads are known as marking sites that are regularly visited by wolves (Barja et al., 2004; Stępniak et al., 2020), which increases the likelihood of detecting entire pack and reproductive events. Cameras with a fast trigger (<0,5 s) and infrared flash were used, set to video mode or to capture image series with a 0–1 s between recordings. This allowed us to better estimate the number of individuals within a group.

2.1.3 Telemetry

In 16 cases (9.1% of territories), GPS telemetry data were used to determine home ranges of residential wolves. Wolves were captured using Belisle 8″ and Victor soft-catch leg-hold traps in three study areas in the Czech Republic (Šumava National Park, České Švýcarsko National Park and the Beskydy Protected Landscape Area). In addition, data from Allensteig military area in Austria were included as some collared animals dispersed and established home ranges in the Czech Republic. Additionally, one wolf was monitored after being released following rehabilitation from a traffic accident in Krušné hory. All animals were equipped with GPS Plus collars (Vectronic AEROSPACE GmbH, Germany). For more details about the trapping procedure and home range estimation, see Vorel et al. (2024).

2.1.4 Public reporting

Some observations and killed wolves were opportunistically reported by the public, foresters and hunters with field verification carried out by state nature conservation authorities or trained persons whenever possible. Dead wolves were examined in the Faculty of Veterinary Medicine in Brno, where additional tissue samples were collected for genetic analysis.

2.1.5 Genetic analyses

DNA from scat and urine samples was isolated using the QIAamp Fast DNA Stool Mini, and in the case of urine, with the protocol according to Hausknecht et al. (2007) with modifications according to Jarausch et al. (2021). For tissue, swab, and hair samples, the DNA mini kit (GENEAID) was used and blood samples were isolated using the blood/cell DNA mini kit (GENEAID), following the manufacturer's protocols. A panel of 21 microsatellite loci and sex-determining gene (amelogenin) was amplified by PCR as described in Hulva et al. (2024). The species status of particular genotypes (aimed to exclude potential fox or dog samples misidentified as wolf samples in the field) was performed using cluster analysis in Structure (Pritchard et al., 2000). The initial burn-in was set to 200,000 steps followed by 1,000,000 iterations of Markov Chain Monte Carlo (MCMC). Analysis was performed using the no-admixture model with uncorrelated allele frequencies and no prior population data. Clusters were tested for K values from 1 to 10, with each K run five times. The results were then uploaded to StructureSelector (Li and Liu, 2018) for visualisation and optimal cluster selection using multiple methods. Using the Cervus program (Kalinowski et al., 2007), identity analysis was conducted with a filtering process requiring at least 14 matching loci and allowing up to five allelic dropout mismatches. Primary data and metadata were checked in all ascertained identical genotypes. The genealogical structure was assessed using ML-Relate (Kalinowski et al., 2006). After identifying the most probable relationship (FS = full siblings or PO = parent-offspring), a hypothesis test with 100,000 simulated genotypes was conducted to evaluate statistical significance. Temporal and spatial data were used to refine these relationships. To validate the results, a maximum-likelihood approach in Colony ver. 2.0.6.6 (Jones and Wang, 2010) was applied, assuming both male and female polygamy. All individuals were considered as potential parents, with a 0.5 probability of inclusion for fathers and mothers and an assumed error rate of 0.01 (Palomares et al., 2017).

2.1.6 Livestock depredation trends

Since there is no central registry of livestock damage caused by large carnivores in the Czech Republic, we individually asked all regional offices and nature conservation bodies for dates, locations, number of wolf attacks and the total number of killed domestic animals in each wolf year.

2.2 Data validation

All occurrence data collected and stored in the database were validated following the guidelines published by Kaczensky et al. (2009) and Kutal et al. (2017), using three categories reflecting the reliability and probability of wolf origin. Category C1 represents hard evidence, such as telemetry data, genetic evidence, a dead animal or clear camera trap pictures; category C2 refers to confirmed data, such as wolf scats or prey remains; and category C3 is associated with unconfirmed data. For further analysis, only records classified as C1 and C2 were considered.

2.3 Data integration in determining family groups and territories

Genetic and telemetry records were used to validate territories identified through field surveys (camera trapping and snow tracking). In the context of this paper, we use the term 'territory' to refer to a home range subset that is used and defended by its holders (in the sense of Maynard-Smith, John, 1974; Mech and Boitani, 2003), as commonly applied in studies about wolves (e. g., Jarausch et al., 2021; Smith and Cassidy, 2024). The centre of each territory was estimated based on the frequency of reproduction events or signs of presence or visits detected by camera traps each year. To illustrate the development of the territories during the study period (Fig. 2), circles with a radius of 8 km were drawn around the centre of each territory, which corresponds to an area of approximately 200 km^2. This method is consistent with the approach used by Nowak & Myslajek (2016) in Poland, based on the average size of territories in Poland of 201 km^2 (Jędrzejewski et al., 2007), a value very similar to 214.3 km determined by GPS telemetry in the Czech Republic and Austria (Vorel et al., 2024). Territories that only marginally (<10%) encroached on the Czech Republic were excluded from further analysis. A total of 163 territories were identified over the 12-year period and were included in the analyses.

Two-thirds of the territories (68.3%) were confirmed by at least two different monitoring methods and approximately one-quarter (25.6%) by at least three. Obtained information on relatedness (FS or PO) was used to ascertain individuals' membership to family groups (packs), and to verify the proposed territories based on field monitoring. An area was considered occupied by a resident pack if at least three wolves were recorded during a wolf year or if reproduction in the pack was confirmed by either method. A territory was considered to have pair status if only two wolves were detected. If only one individual was repeatedly sighted throughout the year, such an area was considered to be occupied by a single territorial wolf. These three categories of wolf territory were based on the monitoring guidelines from Germany (Kaczensky et al., 2009). Sporadic or anecdotal occurrences were excluded from analyses of possible territories, since these may result from dispersal events from natal packs or from individuals acting as floaters The minimum number of individuals was estimated in autumn and winter using one of three methods: camera traps (85 cases), snow tracking (50 cases), or a combination of the two (33 cases). All integrated data are available in Table S1.2. The average elevation of wolf territories was calculated by zonal statistics in QGIS (QGIS.org, 2023) over the Continental Europe Digital Terrain Model at 30 m resolution (Hengl et al., 2020).

2.4 Model of data trends

Population development (described as the number of territories over time) was evaluated separately for two populations defined a priori according to geographic range (the Central European population, which occurs throughout most of the country, and the Carpathian population, which occurs in the Western Carpathian Mountains in the eastern part of the Czech Republic; see the division line in Fig. 1).

Bayesian state-space models implemented in JAGS were used to describe and quantify the trend in the number of wolf territories, wolves, killed livestock and wolf attacks. A process model described population dynamics and an observation model accounted for observation error. The true population size N_t was modelled as a stochastic process, with population growth determined by a finite rate of increase λ and process noise. The population growth followed a log-normal distribution:

$$log\left(N_{[t]}\right) = \lambda \cdot N_{[t-1]} + \varepsilon$$

where ε was normally distributed with variance σ_{proc}^2 representing process noise. The observed population size $N_{obs[t]}$ was modelled as a Poisson random variable with a gamma-distributed mean λ_{Nobs} that depends on the true population size with an observation error. The mean and variance of λ_{Nobs} were calculated as:

$$\lambda_{Nobs[t]} \sim \Gamma\left(shapeObs_{[t]}, rateObs_{[t]}\right)$$

Where

$$shapeObs[t] = \frac{N_t^2}{\sigma_{Obs}[t]^2}$$

and

$$rateObs[t] = \frac{N_t}{\sigma_{Obs}[t]^2}$$

with $\sigma_{obs[t]}$ being an observation error. Uninformative or weakly informative priors were assigned to all parameters. Data input of all models were the observed time series N_{obs} of either number of wolf territories in the Carpathian and lowland population, individual wolves in the Carpathian and lowland population, killed livestock or wolf attacks. Six parallel Markov Chain Monte Carlo (MCMC) chains were run, each with 100,000 adaptation iterations followed by 1,000,000 sampling iterations. A thinning interval of 10 was applied to reduce autocorrelation. Convergence of the MCMC chains was assessed using the Gelman-Rubin diagnostic, ensuring $\hat{R}$ values were close to 1 for all monitored parameters. All analyses were conducted using R version 4.4.2 (R Core Team, 2024) and JAGS version 4.3.2 (Plummer, 2003).

2.5 Population density

We estimated the population density of wolves in areas occupied by a pack based on the average size of home ranges in Central Europe (Vorel et al., 2024) and data from our study (102 observations from 31 packs). To obtain a robust estimate, 10,000 Monte Carlo simulations were performed using the mean pack size per wolf pack (n = 31) combined with known territory sizes (n = 16) to calculate average wolf density with 95% confidence intervals. All analyses were conducted in R version 4.4.2 (R Core Team, 2024) using the *dplyr* package.

2.6. Pack size

A generalized linear mixed model (GLMM) with a Poisson distribution was used to test differences in pack size between early (first and second year) and late (third to sixth year) periods. Territory identity was included as a random effect to account for repeated measurements within packs. Analyses were performed in R version 4.4.2 (R Core Team, 2024) using the *emmeans* package to estimate marginal means and test contrasts.

3. Results

The first pair of wolves occupied the border area with Germany in the Hohwald region in 2011/2012, and the first inland pack was established in the lowlands of central Bohemia in 2014/2015. In the following years, wolves gradually expanded into the mountainous regions along the borders of the Czech Republic with Germany and Poland, finally occupying most of these mountainous areas (Fig. 2). In 2022/23, out of 40 territories in total, 30% were inland, 30% were shared with Germany and 27.5% were shared with Poland. The remaining 7.5% and 5% were shared with Slovakia and Austria, respectively. Most of the country was occupied by the Central European population, while the Carpathian wolves colonised only the north-eastern part of the country, which belongs to the Western Carpathians (see the division line in Fig. 1 and Fig. 2 for the attributions). There were five cases of dispersal of Carpathian wolves into ranges of Central European lowland wolves and four cases vice versa (Fig. 1). A total of 163 territories were identified over the 12-year period.

From 2011/12 to 2022/23, the annual growth rate of wolf territories was $\lambda = 1.25 \pm 0.18$ (0.92–1.68) in the Carpathian population and $\lambda = 1.39 \pm 0.08$ (1.22–1.57) in the Central European population (Fig. 3). The difference between the two growth rates was substantial with only 41% overlap between the two posterior distributions (Fig. 3). The annual growth rate of the number of individual wolves from 2011/12 to 2022/23 was $\lambda = 1.50 \pm 0.20$ (1.15–1.98) in the Carpathian population and $\lambda = 1.50 \pm 0.10$ (1.31–1.73) in the Central European population (Fig. 3). The difference between the two growth rates was smaller with the two posteriors having a 78% overlap (Fig. 4).

The growth rate of the number of wolf attacks on livestock in the Czech Republic over the same period was $\lambda = 1.48 \pm 0.14$ (1.23 – 1.80) while the growth rate of the number of killed livestock increased by $\lambda = 1.51 \pm 0.19$ (1.18 – 1.94) (Fig. 5). The growth was larger than territory growth but the pattern was more irregular as indicated by wide credible intervals.

The average wolf density in areas occupied by a wolf pack was estimated to 4.19 ± 0.49 ind./100 km^2 (95% CI: 3.29–5.2). Wolf pack sizes (n = 102) ranged from 3 to 11 individuals during autumn and winter, with a mean of 5.70 (± 0.24, 95% CI: 5.22–6.17). The minimum number of wolves per territory increased from 2 in 2011/2012 to 4.95 ± 1.91 in 2022/2023 ($r_S = 0.63$, $p = 0.028$), while the overall average pack size remained stable throughout the study ($r_S = 0.40$, $p = 0.228$). However, it is notable that packs in their first and second year were significantly smaller (mean 4.95; 95% CI: 4.4–5.56) than packs occupying a territory from the third year onwards (mean 6.61; 95% CI: 5.91–7.39; $p < 0.001$; see Fig. 6 and more details in Supplementary material: Table S1.3 and Fig. S1.4).

The average elevation of wolf territories increased from 391.7 (±49.3) m a.s.l. in 2011/2012 to 665.2 (±220.6) m a.s.l. in 2022/2023, and the range (min – max elevation) changed from 274 – 581 to 116 – 1502 m a.s.l. Excluding Carpathian territories yields a very similar trend, with a mean altitude of 666.8 ± 230.1 m a.s.l. in 2022/23 (see Tables S1.5 and S1.6).

A total of 27 cases of wolf mortality were recorded, none of which involved collared wolves. Of these, 19 (70.4%) resulted from traffic collisions, five (18.5%) from shooting or snaring, one (3.7%) from being killed by another canid (probably another wolf), and in two cases (7.4%) the cause of death was unknown (see Table S1.7 for details). Among the 26 cases with known sex, 46.2% were males and 53.8% females. Of the 24 cases with known age, 25% were young (<1 year) and 75% were adults. Among 18 cases with known social status, 69.2% were dispersers and 30.7% residents. Significantly more dispersers were killed in traffic collisions than by other causes of mortality (Fisher's exact test, one-tailed, $p = 0.032$, OR = 7.50, 95% CI = 1.19–∞).

4. Discussion

The development of the wolf population in the Czech Republic from 2011/2012 to 2022/2023 showed exponential growth in both the Central European and Carpathian populations, being higher in the Central European population. This pattern mirrors the trend observed in neighbouring western Poland (Nowak and Mysłajek, 2016) and Germany (Reinhardt et al., 2019), although the Czech Republic was colonised a decade later. Until 2013, only sporadic wolf occurrences were reported in the Czech Republic (Kutal et al., 2017) despite forests – the most preferred habitats (Vorel et al., 2024) – covering a slightly higher percentage of the landscape than in Germany and Poland (Eurostat, 2024), and despite a moderate human population density (133 people/km2; Czech Statistical Office, 2022).

We assume that the delayed recovery of the Central European population in the Czech Republic may have been influenced by the complex relief of mountain ranges forming much of the country's northern border, and that changing habitat preferences of wolves could have subsequently facilitated their colonisation of a substantial part of the hilly Czech landscape. The mean elevation of wolf territories increased by more than 250 meters during the study period, which distinguishes the first pioneers from Germany and Poland, where the majority of wolves occupy the lowlands (Kaczensky, 2018). New colonisers may prefer to settle in an area with similar habitat characteristics (natal habitat-biased dispersal), especially when dispersal distance is short (Sanz-Pérez et al., 2018). Indeed, the origin of the first breeding female was traced up to 60 km into Germany (Dauban, Saxony), supporting the natal habitat-biased dispersal hypothesis. As the available habitat for wolves in the Czech Republic tends to be mountainous (Romportl et al., 2017), wolves dispersed to habitats at higher altitudes situated along the state borders and gradually changed their original preference from flat areas. Another reason for delayed establishment of the first packs in relation to Germany and Poland might be higher mortality due to poaching, which is hard to detect (Liberg et al., 2012). The attitudes of Czech hunters towards another large carnivore, Eurasian lynx (Lynx lynx), is overly negative with 10 % of hunters admitting illegal killing by themselves (Červený et al., 2019). While there are no similar studies on wolves among hunters, wolves appear to be perceived more negatively than lynx by local people in the Czech Republic (Opdam et al., in press). Wolves in Germany had high survival rates between 2001 and 2020 (Planillo et al., 2024) and were perceived mostly positively within society after 17 years of co-existence (Arbieu et al., 2019). Although our dataset did not enable us to calculate survival rates, the survival in the Czech Republic might be lower due to the fact that small packs recorded in the first two years were significantly smaller than those recorded later on, as discussed in more detail below.

The mean annual territory expansion rate of 39% in the lowland was comparable with the growth reported in neighbouring countries (30%; Mysłajek et al., 2018; 36 -38 %; Nowak and Mysłajek, 2016; 32%; Planillo et al., 2024; 36%; Reinhardt et al., 2019). This was also higher than that observed in other recolonising populations such as in the Alps (22%; Marucco et al., 2023) and the Scandinavian population (29%; Wabakken et al., 2001) but comparable to the the Great Lakes region of the USA (29%; Van Deelen, 2009) and the Yukon region of Canada (49%; Hayes and Harestad, 2000).

The growth of the Carpathian population was different from the Central European population, and started 6 years later. The first wolves were already documented in the Czech Carpathians in the mid-1990s, and although the nearest territories in Slovakia were located 10-50 km from the border (Kutal et al., 2016; Nowak et al., 2008), no stable territories were confirmed before 2017. Legal killing of wolves in Slovakia may have influenced the recolonisation process (Kutal et al., 2016). Restrictions of killing introduced in 2013/2014 including quotas, expanded areas with year-round protection and field verifications of killed wolves (Bartošová and Kutal, 2014) may have facilitated the wolf dispersal to the Czech Republic. The growth rate of the population size (measured by minimal number of wolves) was similar as in the Central European population, but the number of territories grew considerably slower compared to the Central European population (Fig. 3). This difference may be related to the Carpathian population's later recovery (i.e., a slower growth rate in the initial phase) or to the fact that the Carpathian population was still under some hunting pressure in neighbouring Slovakia until 2021 (Kutal et al., 2024).

When monitoring large areas, some packs may go unnoticed and wolf territories in regions without regular surveys may be overlooked. When the first wolves recolonised the Beskydy

Mountains in the mid-1990s, they attracted significant media attention, and the loss of unattended livestock caused considerable public concern (Kutal et al., 2018). In modern times, small herds of livestock are widespread in the Czech countryside, and the long absence of wolves combined with inadequate preventive measures have made sheep and goats in particular easy prey (Kovařík et al., 2014; Singer et al., 2023). Livestock losses caused by wolves, particularly in early phases of population establishment, may provide a useful indicator of wolf expansion in areas without a long-term wolf presence and with limited resources for wolf monitoring. Indeed, overall trends in wolf presence and livestock damage were very similar throughout the study period.

The higher growth rate of livestock damage compared to the growth rate of wolf territories also suggests that farmers located at a wolf recolonisation front have not adapted their grazing systems to the changing conditions and therefore suffer from high damages. Wolves are territorial, but livestock distribution is clustered, farms without sufficient preventive measures provide a regular food source for nearby packs, and the volume of damage can increase much faster than the number of territories. In Germany, the number of sheep killed by wolves increased by an average of 41% per year between 2002 and 2019, driven by the expansion of the wolf population, suggesting insufficient prevention measures (Khorozyan and Heurich, 2022). Territories and damage incidents grew at comparable rates between 2018–2020 (Singer et al., 2023), but this period followed more than 15 years of wolf presence in the country (Reinhardt et al., 2019). Contrasting results were obtained from Italy, where chronically recurring and increasing damages were reported in areas of historical distribution in the central-southern part of the country, while decreasing damages occurred in the recently recolonised northern regions (Gervasi et al., 2021). Recurring damage indicated a dysfunctional system in which compensation is paid regardless of preventive measures (Gervasi et al., 2021). A similar system exists in the Czech Republic: although financial support is available for preventive measures and additional work related to wolf presence, damage compensation is paid regardless of their quality of implementation of preventive measures (Pelc, 2024). This may create a moral hazard whereby there are few incentives to increase herd protection as damage compensation is provided regardless.

The published average size of wolf packs in Europe varies substantially, from 2.7–3.2 up to 7.5–8 individuals (Jedrzejewski et al., 2000; Mysłajek et al., 2018; Nowak et al., 2024, 2008; Okarma et al., 1998). Our mean value of 5.7 thus falls within this range. However, packs occupying the area for at least three years were considerably larger. The average size of such packs (6.7) was almost identical to resident packs persisting for at least three years in western Poland (Nowak and Mysłajek, 2016). A wolf pack in its second year, during autumn and winter, typically consists of a breeding pair, pups (<1 year old), and yearlings (>1 year old; Mech and Boitani, 2003). However, our study revealed that packs in their first and second year were of similar size, and pack size increased only from the third year of breeding onwards. This indicates that breeding pairs may require more time to adapt to a new environment and/or suffer from high mortality during the first years of recolonisation.

The estimated population density of wolves (4.19 ± 0.49 individuals /100 km^2) represents the first published estimate for the Central European population. This value is comparable with those reported from the Polish Carpathians (3.3 - 5.1; Smietana and Wajda, 1997) and Northern Apennines (4.7; Apollonio et al., 2004) but lower than recent estimates from the Romanian Carpathians (2.35; Iosif et al., 2025), north-western Poland (1.2; Mysłajek et al., 2018) or Spain (2.5; Jiménez et al., 2023; López-Bao et al., 2018). However, studies vary in their methodological approach, the robustness of their analyses, and whether they calculate the value for the whole study area or only the areas occupied by packs. Our value is in the higher end of the reported range because it refers exclusively to areas permanently occupied by packs (i.e., excluding areas occupied by pairs or single territorial wolves). On the other hand, it does not account for dispersing wolves, which may be detected through non-invasive genetic sampling, as our calculations were based on the number of pack members in late summer and winter.

Known mortality of Czech wolves was predominantly anthropogenic, with traffic collisions representing the most frequent cause, similar to findings from Germany and western Poland (Nowak and Mysłajek, 2016; Reinhardt et al., 2019). The relatively high proportion of dispersers among traffic deaths contrasts with the absence of detected dispersers among illegally killed wolves, although the sample size was small and many poaching events were likely undetected (Nowak et al., 2021; Sunde et al., 2021). Juvenile and subadult wolves had lower survival rates than adult wolves in Germany (Planillo et al., 2024) and dispersers suffered higher mortality than resident wolves in packs in Spain (Blanco and Cortes, 2007). Cases of illegally killed wolves were recorded only rarely in the Czech Republic, as well as cases of natural mortality.

The overall positive trend of the Czech wolf population is remarkable, given its sporadic or even complete absence from parts of the country in previous decades (Kutal et al., 2016). However, our analysis of demography and population dynamics revealed a 10-year delay in recovery for the Central European population compared to Germany and Poland and an additional 6-year delay for the Carpathian population as well as relatively small packs during the first two years after establishment. This suggests that the recovery may have been influenced by the changing preferences within the Central European population to different environmental conditions and anthropogenic mortality, either legal (i.e. killing of wolves in neighbouring Slovakia for the Carpathian population), illegal, or a combination of all. With the wolf protection status in the EU having been downgraded from strictly protected to protected (Kutal et al., 2025), there is a non-negligible risk that killing—now no longer to be justified on an individual basis—becomes liberalized and threatens the long-term recovery of this population. In this context, the integration of genetics, camera trapping, telemetry, and field surveys, combined with substantial support from citizen science, which our study has presented, can provide monitoring information that is vital for the conservation of this expanding population.

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