

The grey wolf (*Canis lupus*) in southwestern Bohemia (Czech Republic): the beginning of new expansion in a long-term perspective

Luděk Bufka^{1,*} & Jaroslav Červený²

¹ Šumava National Park Administration, Sušická 399, CZ-34192, Kašperské Hory, Czech Republic

² Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká 129, CZ-16500 Praha 6, Czech Republic

* ludek.bufka@npsumava.cz

Abstract

Long-term monitoring data were analysed in order to describe the development of the grey wolf occurrence in the southwestern Czech Republic. Altogether, 638 occurrence records from 1950–2018 (till 30 April 2019, resp.) were collected. The occurrences during the long period 1950–2014 had a mostly episodic character. The new and real wolf recovery started in the wolf breeding years (WYs) of 2014–2018. 83 % of all records fall into this period, the number of occurrence data increased sharply during these five seasons. The number of grid mapping squares with confirmed occurrence (C1, C2 data) increased from 1 in the WY 2014 to 37 in the WY 2018 (0.6% to 21% of the study area). The first reproduction was confirmed in the WY 2017. The red deer represents the main prey item, based on accidental kill findings. The rapid increase of financial compensations paid for the damages to livestock also illustrates the wolf expansion. There is a tendency of stabilization of the permanent occurrence in forested border regions. The documented process represents the beginning of wolf recovery (in the sense of stable occurrence and reproduction) in the region ca. 150 years after extermination of the original population.

Key words: grey wolf, southwestern Bohemia, occurrence, distribution, population recovery

INTRODUCTION

At present, the phenomenon of recovery of large carnivores at many places across Europe where these animals did not occur for tens or hundreds of years is often reported. Generally, the total area of distribution of all European large carnivore species, i.e. of the Brown bear (*Ursus arctos* L.), Eurasian lynx (*Lynx lynx* L.), Grey wolf (*Canis lupus* L.) and also of the Wolverine (*Gulo gulo* L.) in northern areas, has indeed been increasing in the last 40–60 years. Nowadays at least one of these species occurs in an area covering about one third of Europe (CHAPRON et al. 2014). Considering the current distribution range of large carnivores in Europe, it is obvious that they live not only in secluded and natural areas, but also in regions with a relatively high density of human population. They inhabit landscapes which are significantly altered, intensively used and fragmented by infrastructure (CHAPRON et al. 2014). Among European large carnivores, the wolf stands out by its ecological adaptability and ability to recolonize even the human-dominated landscapes (MECH & BOITANI 2003).

The wolf, as a native species, probably used to be widespread throughout Bohemia. Similarly as other large carnivores, it was intensively persecuted and hunted by man in the past. As a result, the wolf was probably uncommon in Bohemia already since the Middle Ages. A temporary increase in the wolf population was recorded in the period of the Thirty Year War (KOKEŠ 1961). In the 18th century, however, the numbers declined again and the species gradually disappeared from many regions (ANDRESKA & ANDRESKOVÁ 1993). In the 19th century, the wolf was still subjected to hunting in Bohemia, however, these were rather rare cases, probably representing vagrant individuals (KOKEŠ 1961). The longest existence of the wolf is documented from the Šumava Mts., where the last individuals from the original population were hunted around the years 1891–1894 (ANDĚRA et al. 2004). During the 20th century, occurrence of the wolf was only sporadic in Bohemia. Somewhat more numerous data come from southwestern Bohemia from the late 1970s and early 1980s, when the occurrence was at least partly related to escapes from captivity (overview in BUFKA et al. 2005). Later on, in the years 1990–2004, a larger number of records were collected in the Czech-Bavarian-Austrian borderland. The wolf presence is stated as a regular occurrence in some synoptic distribution maps for this period (ANDĚRA & ČERVENÝ 2009). However, those data did not provide evidence of permanent occurrence with reproduction (BUFKA et al. 2005). A different situation always was in the eastern part of the Czech Republic, where the wolves still occurred more frequently and continuously during the 19th century (ANDRESKA & ANDRESKOVÁ 1993). The presence of the species in this region has always been dependent on the status of the Carpathian population in the neighbouring Slovakia and Poland. The wolf started to be registered there again after 1945, then gradually established islands with regular occurrence in more forested areas, especially the Czech part of the westernmost Carpathians (ČERVENÝ et al. 2000, BARTOŠOVÁ 2001). The existence of 2–3 reproducing pairs or small packs was estimated in the period 1994–2000 (ANDĚRA et al. 2004). Nevertheless, only sporadic occurrence was found out in the following period 2003–2012. The stagnation of the West-Carpathian population influenced by wolf hunting in Slovakia is assumed to be the main reason of this pattern till the latest period (KUTAL et al. 2016b, 2017).

A quite new phase of the wolf occurrence in Bohemia began after the year 2000, when the wolves started to reappear, first mainly in northern Bohemia (FLOUSEK et al. 2014). This process was induced by the increasing population numbers in northeastern Europe and Poland (NOWAK & MYSLAJEK 2016) and consequent spreading of individuals from the population in eastern Saxony-Upper Lusatia, i.e. expansion of the so-called Central-European lowland population (REINHARDT et al. 2019). In several areas of Bohemia, permanent occurrence was established gradually. The first reproduction was confirmed in the Ralsko former military training area, Česká Lípa region, in 2014, then in the Broumov region and the Krušné hory Mts. in 2016. Besides reproduction, permanent occurrence was registered also in the Šluknovský výběžek Hook and Frýdlantský výběžek Hook (northernmost Bohemia) within the period 2012–2016. Simultaneously, an increasing amount of records of sporadic occurrence were collected, including those from southern and western Bohemia (KUTAL et al. 2017, ANDĚRA & GAISLER 2019). This paper summarises all available information on the beginning of wolf expansion in southwestern Bohemia, as an important region for large carnivores with a relatively high natural potential, and evaluates this status in the context of long-term development of the wolf population in this region. On the contrary, occurrence of the wolf in this region after the year 2018 is not evaluated, as it is considered permanent.

MATERIAL AND METHODS

Study area

The area under study includes the southwestern part of the Czech Republic, lying within the boundaries of the Plzeň and South Bohemian Regions. This territory covers the mutually linked forested areas situated in the line (from northwest to southeast) of the Český les Mts. – Šumava Mts. – Novohradské hory Mts. – Třeboň region, as well as the connecting corridors in the northern direction to the Slavkovský les, Doupovské hory and Krušné hory Mts., in the northeastern direction to the Brdy Mts. and in the eastern direction to the Českomoravská vrchovina Highlands (Fig. 1). It is an important core area and migration corridor for large carnivores (e.g. ANDĚL et al. 2010).

The forest coverage in the study area is higher (40.6% in the Plzeň region and 38.1% in the South Bohemian Region) compared to the mean coverage in the whole Czech Republic (34.1%) (MZe ČR 2019). The study region includes large compact areas with forest cover reaching up to 80%, such as the Šumava National Park. Several forested large-scale protected areas are situated in the study region: the Šumava National Park (NP) and Protected Landscape Area (PLA), Český les PLA, southwestern part of the Brdy PLA, Blanský les and Třeboňsko PLAs. Large-scale protected areas make up altogether ca. 18% of the study area.

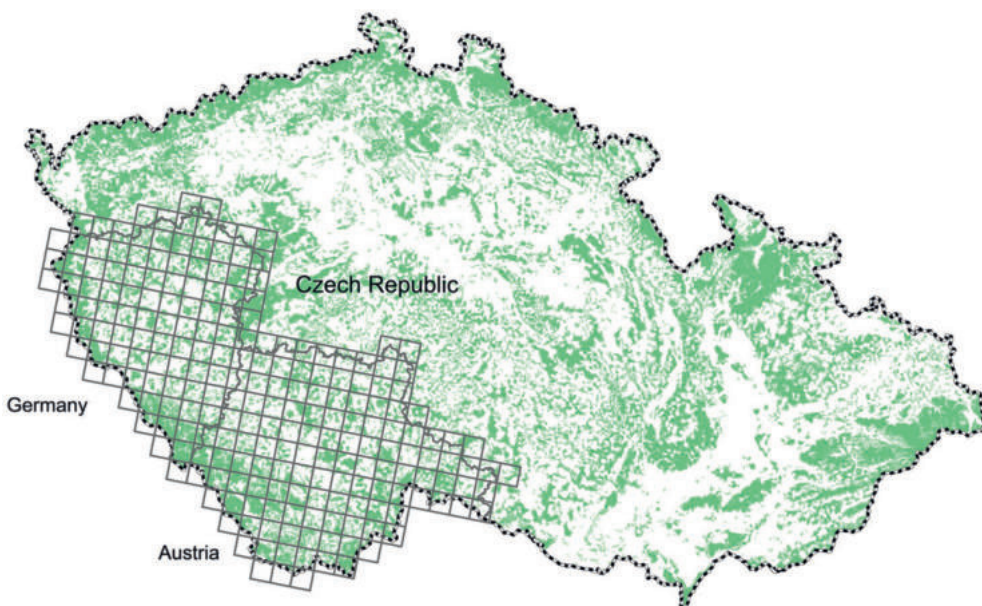


Fig. 1. Map of the Czech Republic showing the area under study (Plzeň and South Bohemian Regions) covered by the respective part of the EEA 10×10 km square mapping grid.

On the other hand, the mean density of human settlement in the study area is the lowest within the country (134 persons per square km), i.e. 76 persons per square km in the Plzeň Region and 64 persons per square km in the South Bohemian Region (ČSÚ 2018).

Data collection and analysis

Summary of all available data obtained in the study area in the period 1950–2018 (till 30 April 2019, more precisely) was used in the analysis. These data included records of all direct visual observations, findings of signs, photos or findings of dead individuals. They were either own findings made by the authors and their co-workers (see Acknowledgements) or records obtained using camera traps and a questionnaire survey. The large amount of data from recent years is a secondary but valuable product of systematic photo-monitoring primarily focused and optimised on the Eurasian lynx population. However, this camera trapping system enables to register also other mammal species including wolf.

For a summary assessment, basic characteristics of the collected data were used, i.e. whether they were a direct visual observation, a finding of signs (footprint or trail, faeces, prey remnants), a photo of an individual, or a finding of a carcass. Besides that, all data were classified within the scale of credibility according to a standard system currently used for large carnivores (SCALP criteria – MOLINARI-JOBIN et al. 2012). Following this method, the occurrence data are classified according to their objectiveness and verifiability into three categories: the C1 category includes “objective evidence of the species occurrence” (cadaver, sample verified by DNA analysis, photo from a camera trap, data from telemetric survey); the C2 category includes “documented occurrence of the species” (e.g. remnants of prey killed by the carnivore or tracks documented and verified by an expert in the field); the C3 category includes “undocumented and unverifiable data” (e.g. visual observation of the carnivore, tracks or remnants of prey reported by the public without documentation). For the assessment of occurrence, distribution and development of the wolf population in recent years, in order to reach maximum objectivity and avoid overestimation, only the C1 and C2 data were used preferentially (*sensu* KACZENSKY et al. 2013, KUTAL et al. 2017). However, a significant improvement in the methods of obtaining objective data has been achieved approximately since the year 2008, with the gradual development in the use of camera traps and genetics in species monitoring. For completeness and also to keep comparability of the occurrence data on a long-term scale, we thus provide also the C3 category data in the summary tables and figures. These data are always shown separately and clearly differentiated, though. As a basic time unit for the assessment of changes in the development of occurrence and distribution, a wolf breeding year (“wolf year”– WY) was used instead of a calendar year, analogous to the reproduction year used for long-term monitoring of the Eurasian lynx or wildcat, which starts on 1 May of the given calendar year and finishes on 30 April of the following year. Special attention was paid to the assessment of the last five-year period (WYs 2014–2018), when simple occurrence, as well as its character regarding persistence of the species occurrence in time and regarding confirmed reproduction, were analysed. The layer of all records was interlaid with the 10×10 km square mapping grid (EEA 2017) for compatibility and possible comparison of the distribution in the European context and with neighbouring countries (Bavaria, Austria). One of the following values / categories of occurrence was assigned to each square for the last period of WYs 2014–2018:

- 1) Permanent occurrence (occurrence of the species in the given square was confirmed at least in three years of the given five-year period).
- 2) Sporadic (temporary) occurrence (occurrence of the species in the given square was confirmed in less than three years of the given five-year period).

RESULTS AND DISCUSSION

Sample size and data structure

Altogether 638 records of wolf occurrence were collected in the study period till 30 April 2019. Of them, 184 were direct visual observations, 230 findings of signs, 83 findings of prey remnants, 128 photos, 13 kills or findings of dead individuals. The long-term population development was summarised in five-year periods (Table 1). Of the total number of registrations, 524 (83%) come from the WYs 2014–2018, indicating a real beginning of recovery of the permanent occurrence in this period.

Concerning provability and verifiability, altogether 172 C1 records, 220 C2 records and 246 C3 records were registered. The overview in five-year periods is given in Fig. 2.

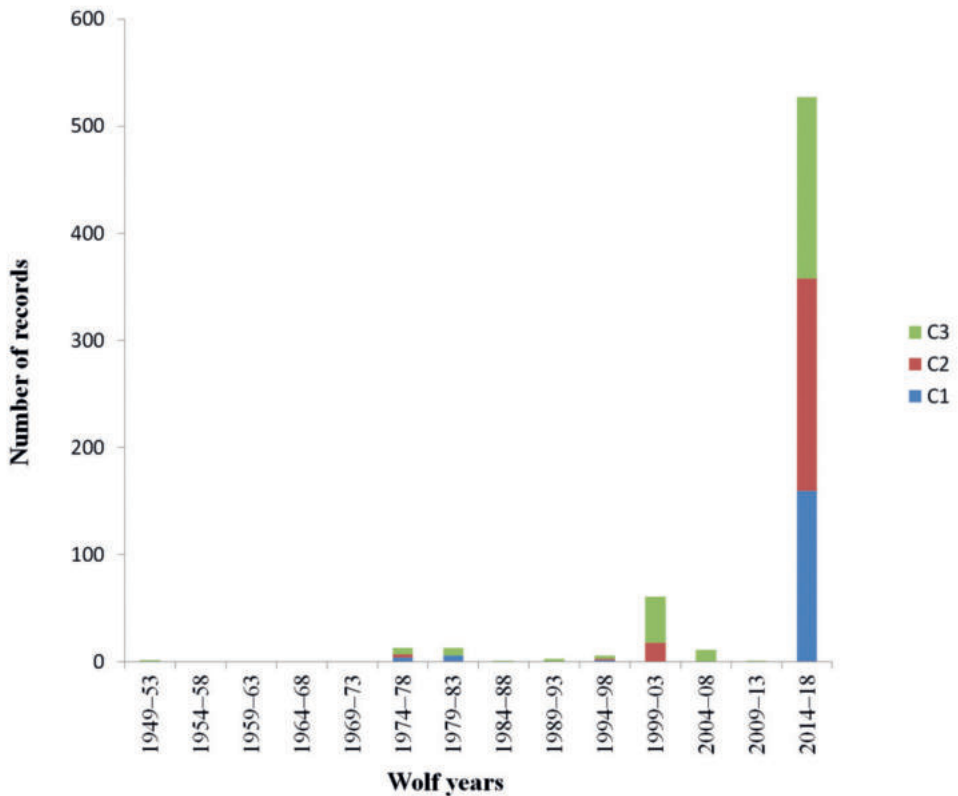


Fig. 2. Map of the Czech Republic showing the area under study (Plzeň and South Bohemian Regions) covered by the respective part of the EEA 10×10 km square mapping grid.

Table 1. Numbers of records of wolf occurrence in 1949–2018 summarised in five-wolf-year periods.

WYs	Visual observation	Signs	Prey	Photo	Cadaver	Σ
1949–1953	1	0	0	0	1	2
1954–1958	0	0	0	0	0	0
1959–1963	0	0	0	0	0	0
1964–1968	0	0	0	0	0	0
1969–1973	0	0	0	0	0	0
1974–1978	4	2	3	0	4	13
1979–1983	7	0	0	0	6	13
1984–1988	1	0	0	0	0	1
1989–1993	3	0	0	0	0	3
1994–1998	1	2	1	0	2	6
1999–2003	17	38	6	0	0	61
2004–2008	5	6	0	0	0	11
2009–2013	1	0	0	0	0	1
2014–2018	144	182	70	128	0	524
Total	184	230	83	128	13	638

Recapitulation of development and current situation

Occurrence of the wolf in southwestern Bohemia can be characterised as rare or sporadic during the whole, more than a hundred-year period between extinction of the original population and the year 2013. From the post-war period, there is practically only one record of a wolf hunted in the Český les Mts. in 1953 (HŮRKA 1981). In the following years, two periods of more numerous records of wolf occurrence in the study area can be traced (Table 1, Fig. 2). The first one was the period 1976–1983, when the occurrence was presumably related to the dispersal of individuals which escaped from captivity in the Bavarian Forest NP. After that, observations on both sides of the border became more frequent and a number of individuals were killed. The total number of captured and killed animals exceeded the original number of individuals escaped from captivity. Some authors thus mentioned possible reproduction in the wild or presence of other wolves in that period (e.g. ANDĚRA & HANZAL 1996). Another period with an increased amount of data on wolf occurrence was approximately between 1990 and 2004. Occurrence in the Czech-Bavarian-Austrian border area in this period was assessed as real, though still sporadic, and it could not be directly related to any other population increase. It probably included single animals only, in two verified cases they were males, reproduction was not confirmed (BUFKA et al. 2005). Concerning the following years 2005–2013, very few data are available from the study area, mostly of the C3 category, despite the more massive use of camera traps started in the Šumava

Mts. for monitoring of the Eurasian lynx and larger mammals already since the winter of 2008–2009 (Bavarian Forest National Park) and 2009–2010 (Šumava National Park) (WEINGARTH et al. 2012, 2015). A marked turn was recorded first in the WY 2014, when the wolves started to appear in camera traps, and the number of accidental observations and findings of signs increased at the same time. The documented process can thus be regarded as the wolf recovery (occurrence of a really permanent character) in the region, about 150 years after the extinction of remnants of the original population. This pattern is apparent in a long-term view, both from the number of records in the particular periods (Table 1) and the total area of distribution expressed by the number of occupied mapping squares (Fig. 3, Table 2).

Detailed analysis of population growth in the WYs 2014–2018

In this period, altogether 524 occurrence records were obtained in the study area, of them 144 were direct visual observations, 182 findings of signs, 70 findings of prey remnants, 128 photos of individuals. Concerning provability and verifiability, 160 C1 records, 198 C2 records and 169 C3 records were registered. The WY 2014 definitely marks a beginning of the modern expansion of the species in the study area (region) and a beginning of permanent occurrence. During the following seasons, the number of occurrence records grew gradually. This increase in the number of registrations in different categories during the WYs 2014–2018 has a steep character (Fig. 4).

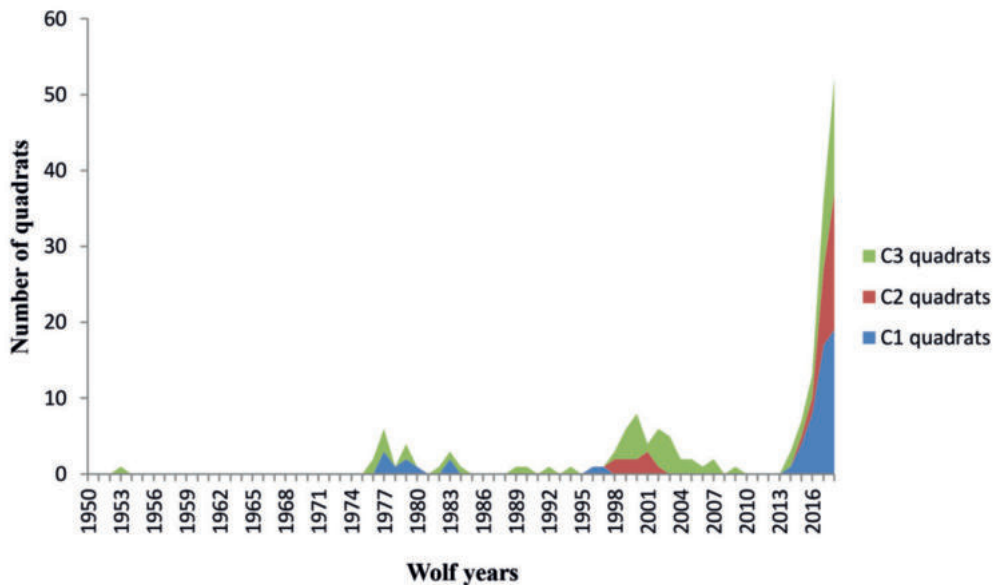


Fig. 3. Area of wolf distribution in southwestern Bohemia in the WYs 1950–2018, expressed by the number of squares occupied by C1, C2 and C3 data.

Table 2. Increase in the number of squares with confirmed wolf occurrence and confirmed reproduction in the successive seasons of WYs 2014–2018. Explanations: *3 juvs. confirmed, potentially 5 juvs.; **pregnant female, (?) juvs. not confirmed.

WY	Confirmed occurrence (number of squares (C1+C2))	Number of reproductions	Number of juveniles
2014	1	0	0
2015	5	0	0
2016	10	0	0
2017	27	1	3–5 *
2018	37	1 (2**)	4, (?)

At the same time, the area of distribution changed dramatically during the WYs 2014–2018. Taking into account C1 and C2 records, only one square (0.6% of the study area) was occupied in the WY 2014 season, five squares (2.8%) in the WY 2015, ten squares (5.7%) in the WY 2016, 27 squares (15.3%) in the WY 2017, and as much as 37 squares (21% of the study area) in the WY 2018 (Fig. 5, Table 2).

During the five-year period of WYs 2014–2018, the occurrence was confirmed (data from C1 and C2 categories) in altogether 46 squares (26.1% of the study area). In further 23 squares (13.1% of the study area), only data from the C3 category are available. Among the 46 squares with confirmed presence of the wolf in the given period, the occurrence can be considered permanent in 7 squares (4% of the study area) and sporadic in the remaining 39 squares (22.1% of the study area). Permanent occurrence was recorded in 3 main parts (geographical units)

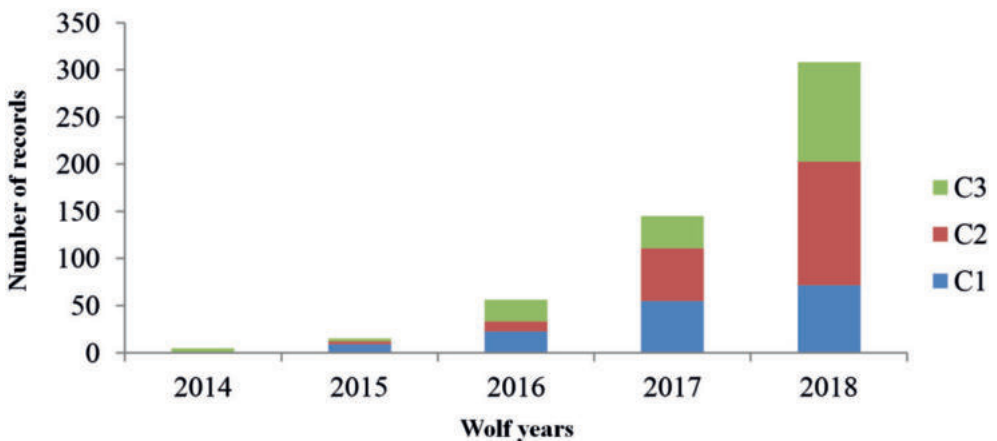


Fig. 4. Increase in the number of wolf occurrence records in the successive seasons (WYs) 2014–2018.



Fig. 5. Spreading of the wolf during the WY 2014–2018 shown in the mapping grid (red – C1 records, rose – C2 records, grey – C3 records only).

of the study area: Šumava Mts. (5 squares), Český les Mts. (1 square), Třeboň region / Javořícká vrchovina Highlands (1 square) (Fig. 6). It is apparent from the maps (Figs. 5, 6) that the occurrence is concentrated predominantly in more forested and relatively low human-populated areas along the border. The permanent occurrence was documented in large-scale protected areas (Český les PLA, Šumava NP and PLA, Třeboňsko PLA).

Reproduction

The first confirmed recent successful breeding of the wolf in the study area was proved in the Šumava Mts in the WY 2017 season. The den was situated on the Bavarian side of the Šumava Mts., in the Bavarian NP. The minimum number of juveniles recorded by photo-monitoring was 3, however, there are certain indications that there might have been up to 5 pups (LfU 2017b, GAHBAUER & HEURICH in litt.). A genetically confirmed fast dispersal of two males from this litter is worth mentioning. Presence of one of them was revealed by the analysis of DNA from saliva left on prey (mouflon) remnants near Arnstadt in Thuringia, ca. 320 km from its birthplace, in April 2018 (e.g. NABU 2018). The other finding was a road kill on the A7 highway, at the Egestorf exit near Hamburg, ca. 600 km from the birthplace, on 3 May 2018 (GAHBAUER & HEURICH pers. comm., LANDESJÄGERSCHAFT NIEDERSACHSEN 2021). In the WY 2018 season, breeding in the Šumava Mts. was very likely (record of a pregnant female),

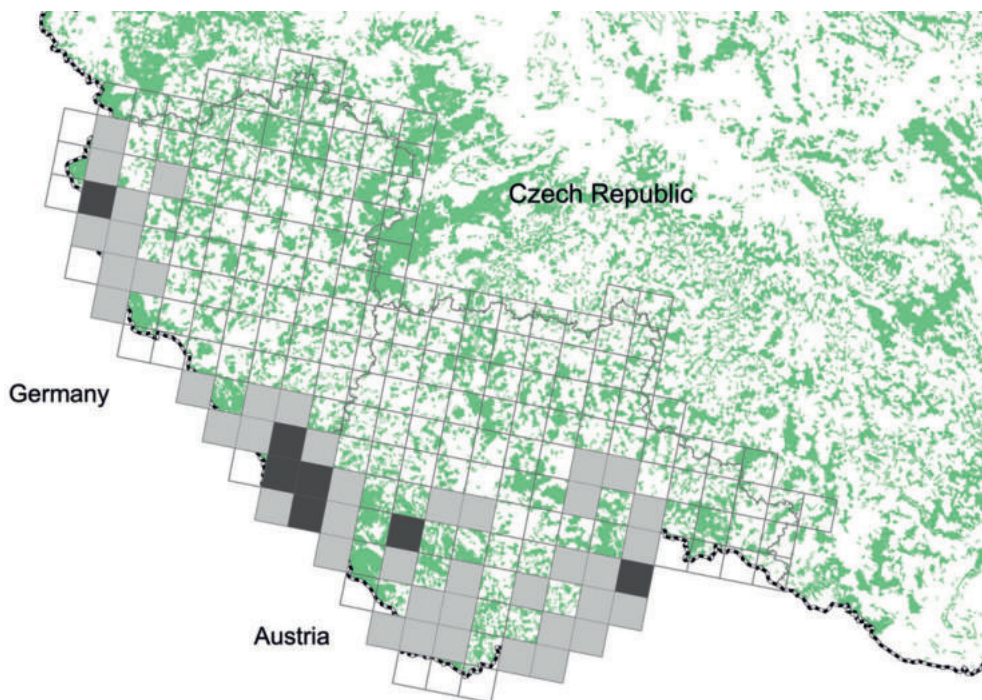


Fig. 6. Permanent (black) and sporadic (grey) occurrence of the wolf in the 5-year period of WYs 2014–2018 (C1+C2 data only).

but its success is unknown, presence of the pups was not proved directly. On the other hand, reproduction was confirmed in the Třeboň region close to the Austrian border in the WY 2018, when at least 4 pups were recorded. In the Šumava Mts., the wolf occurrence got a permanent character in a relatively large area during the five-year period.

In the WYs 2014–2018, reproduction was thus confirmed in two subareas (geomorphological units) of the study area – in the Šumava Mts. and in the Třeboň region / Javořícká vrchovina Highlands, within the territories of large-scale protected areas (national park, landscape protected area).

Origin of individuals

As a result of the gradual increase in numbers and range expansion of European populations of the wolf during several recent decades (CHAPRON et al. 2014), Central Europe including the Czech Republic and our study area became a potential and actual crossroad for spreading of the wolf from different source populations (HULVA et al. 2018). The habitat capacity and suitability for wolf in southwestern Bohemia is relatively high and the functioning interconnection between populations seems to be still possible, although the landscape fragmentation rate has been increasing dramatically in the last ca. three decades (KUTAL et al. 2016a, ROMPORTL et al. 2017). During the theoretical assessment of possible occurrence of the wolf and modelling of carrying capacity of the Šumava area for this species in the early 1990s, the nearest Carpathian wolf population was considered as the only potential source (LANGHAMMER 1993). In the analysis of wolf occurrence in the Czech-Bavarian-Austrian borderland in the year 2004 (BUFKA et al. 2005), the Carpathian population was still evaluated as the most real source, the newly established population in Saxony and Upper Lusatia as less probable, while immigration from the south from the Alps did not seem too real at that time. During the following ten years, the situation started to change dynamically. The Carpathian population still did not show tendency to spread (KUTAL et al. 2017), but on the other hand, a significant increase in numbers and spreading of wolves from the so-called Central-European lowland population occurred (NOWAK & MYSLAJEK 2016, REINHARDT et al. 2019). Most wolf records in southwestern Bohemia are probably related to this trend. However, genetic analyses show that e.g. the female from the first breeding wolf pair in the Šumava Mts. belongs to the Central-European lowland population, while the male to the Italian-Alpine population (LfU 2017a). This documents dispersal abilities of the wolf in human-dominated and urbanised landscape, and supports the fact that at present, the study area (and the Czech Republic and Central Europe as a whole, HULVA et al. 2018) can play a role of a genetic crossroad for individuals from different populations. The above described occurrence and reproduction of the wolf in the Třeboň region may be interconnected with the existence of a pack in the neighbouring Waldviertel area in Austria. The reproduction was confirmed there (in the Allentsteig military area) already in 2016 (WWF 2016). A wolf female was radio-tagged there in June 2019 by experts from the Veterinary University in Vienna. This female left its mother territory at the end of the year, set out northwest and crossed the whole of our study area – the Třeboň region, Novohradské hory foothills, Šumava foothills and Šumava Mts. – in the period between 22 December 2019 and 3 January 2020, and then went very fast northward past Plzeň, through the Křivoklát region to the Žatec area and then westward to the Doupovské hory Mts. (11 January 2020), where she established her territory in the former military

Table 3. Summary of confirmed wolf kills found by chance in the study area during the WYs 1976–2018. Explanation: * female elk consumed by wolf, but killing by wolf was not proved.

WY	Wild boar			Red deer			Roe deer			Sika deer			Elk		Fallow deer			Mouflon					
	M	F	juv un all	M	F	juv un all	M	F	juv un all	M	F	juv un all	M	F	juv un all	M	F	juv un all	M	F	juv un all		
1976		1	1	2																			
1977						1	1																
1999			1	1																			
2000		1	1	1																			
2001		1	1	1	1	1																	
2015					1	1																	
2016		1	1	2																			
2017	1	2	2	5	3	3	1	1	2														
2018	1	5	5	10	1	2	1	5	1	3	1	1	6	1*	1	2	1	1	5	1	1	3	
total	2	4	1	22	3	2	1	11	5	2	3	2	8	1	1	3	2	2	8	1	1	1	4

area (HNUŤÍ DUHA OLMOUC 2020). After all, immigration of individuals of Carpathian origin to southwestern Bohemia cannot be excluded either, as suggested by the finding of a Carpathian wolf killed on the D1 highway in the Českomoravská vrchovina Highlands in the spring 2017 (HULVA et al. 2018).

Predation on wildlife – survey of killed prey

The grey wolf is a typical food opportunist. The diet composition depends mainly on the local food availability (e.g. NOWAK et al. 2011, ČERVENÝ et al. 2019). Altogether 61 specimens of wild animals killed by wolves were recorded (Table 3): 22 *C. elaphus* individuals. (33.3%), 11 *C. capreolus* inds. (18.0%), 8 *C. nippon* inds. (13.1%), 8 *D. dama* inds. (13.1%), 7 *S. scrofa* inds. (11.5%), 5 *O. musimon* inds. (8.2%) and 1 *A. alces* individual (1.6%) in the period WY 1976–2018. The overwhelming majority of the samples (86.9%) comes from the period of recent fast growth of the wolf population, i.e. from the WYs 2016–2018. The recorded consumption of an old elk female may be an important finding due to low density of elks in unique isolated micropopulation in this area (JANÍK et al. 2020). However, hunting by the wolf is not certain in this case, since the used cadaver (with ribs and joint heads of long bones bitten off) was found near a frequented road which is often crossed by the elks and where several dead individuals have been found already after car collision. The relatively low proportion of the wild boar is surprising. Used method is based on accidental findings of prey so it is likely possible that the methodology influenced the results. Expansive analyse of scats samples need to be done in this area for better understanding of wolf prey spectrum. However, a similar finding was published also from the WYs 1999–2003 in the Šumava region: *C. elaphus* (57.1%) and *C. capreolus* (14.3%), while *S. scrofa* was not registered at all (FEJKLOVÁ et al. 2004). Anyway they identified *S. scrofa* as the most frequent prey (F 27.5%) based on analyse of 8 wolf scats followed by *C. elaphus* (F 25%), *L. europaeus* (F 25%) and *C. capreolus* (F 12.5%). These data need to be taken as indicative only, considering the very small number of samples. A similar surprisingly low proportion of the wild boar in the wolf diet was recorded during an intensive survey in the Ralsko u Mimoně region in the period 2014–2018 (ČERVENÝ et al. 2019). Altogether 653 cadavers were included in the analysis. The most frequently hunted species was *D. dama* (35.1%), followed by *O. musimon* (25.1%), *C. capreolus* (21.1%), *C. elaphus* (10.6%) and *S. scrofa* (8.1%). Anyway those results are also based on the same prey findings methodology.

Predation on livestock

Negative perception of the wolf is historically connected mainly with livestock depredation. These animals, especially sheep, unless protected effectively, become a very easy prey for the wolf (e.g. LINNÉL et al. 1996, GULA 2008). In the study area, wolf attacks on livestock have been documented since the year 2004 (Table 4). Compensations paid for livestock killed by the wolf show a significantly upward tendency (Table 4). This trend well co-illustrates the increase in wolf numbers in the region (and, at the same time, an absence or insufficiency of preventive measures in safeguarding livestock during the wolf comeback). Provable damages to livestock are compensated by the government via regional authorities. In the years 2005–2017, no damages were claimed. Proving the causal agent is not always easy, and not all reimbursed damages were actually caused by the wolf. Some kills of farm animals are

Table 4. Paid compensations for damages (in CZK) caused by the wolf on livestock in the Plzeň and South Bohemian regions; in the calendar years 2005–2017, no damages were claimed.

Year	Plzeň region		South Bohemian region		Total	
	CZK	Number of cases	CZK	Number of cases	CZK	Number of cases
2004	39 820	3	0	0	39 820	3
2018	211 148	7	138 000	2	349 148	9
2019	593 608	23	1 277 086	15	1 870 694	38
Total	844 576	33	1 415 086	17	2 259 662	50

caused by feral dogs (compensations are not paid in such case) or by the Eurasian lynx (compensations are paid). Moreover, an unknown proportion of attacked farm animals are not evidenced by the breeders at all for different reasons. Despite that, the payment of compensations can be considered as an additional indicator of the increasing trend in wolf occurrence.

CONCLUSION

The current trend of the wolf expansion in Europe documents that the existence and conservation of populations of top predators is possible even in a landscape significantly altered and densely populated by man. Large carnivores do not need only “wilderness” for life. Generally, their occurrence cannot be restricted to protected areas, although these territories often play an irreplaceable role as core areas. This is also apparent within our study area, where the wolf, even though quite adaptable, occurs and permanently inhabits mainly natural forested areas and large-scale protected areas at first. The results suggest that all post-war occurrences of the wolf in the study area fall into the category of episodic events. However, it is obvious that especially in the 1990s, there already were indications of natural immigration of single animals. Recent recovery of the wolf and the onset of permanent occurrence including reproduction falls into the period since the WY (wolf year) 2014 and is significant from the perspective of long-term development. The number of records, their character and permanency of occurrence in the WYs 2014–2018 is a new phenomenon, 83% of the occurrence data after the year 1950 come from the latter period. Therefore, the wolf recovery seems to be real, though the increase in the number of occurrence records in the last decade is supported by a larger qualitative and quantitative development of the monitoring effort (especially with the use of non-invasive and, at the same time, reliable methods – photo-monitoring and genetic monitoring). Forested border areas, important for the survival of native species of forest mammals, besides other things, have naturally become the main areas of recent wolf occurrence. Especially in the Šumava Mts., the occurrence already shows a permanent character including reproduction. Prediction of further development is difficult; however, regarding the current status and dynamics of wolf populations in Europe, continuing spreading and establishment of other pairs and packs

can be definitely expected in the near future. Landscape capacity and food potential of southwestern Bohemia for the wolf is relatively large. The human attitude/influence in a wider geographical and socio-economic context might thus be the decisive factor for the future wolf occurrence in the area.

Acknowledgement. The authors would like to express their gratitude to the following colleagues for providing summary data and/or for their significant share in field monitoring and providing individual own data (in alphabetic order): Adam O., Assmann B. jun., Assmann B. sen., Assmann M., Babor H., Babor J., Bečka P., Bednářová H., Belotti E., Bešťák J., Bláha J., Bláhová M., Černý R., Červenka J., Drha M., Dvořák R., Falková K., Faschingbauer P., Fridrichová K., Green P., Hátle M., Hejralová J., Hovorková J., Hřebek V., Hubený P., Husinec V., Chlada V., Ježek M., Jirsa A., Kočandrlé J., Kojzar P., Kopačka J., Koranda T., Koubek O., Kratochvíl M., Kůs F., Lupták J., Machálek A., Maschke M., Melichar V., Mináriková T., Mokry J., Nedvěd P., Netrvalová K., Neudert J., Pavliska P., Pechoč V., Pena L., Poledník L., Pospíšil L., Procházka J., Prokopová M., Randák J., Rektoris L., Romportl D., Roubal R., Rüt M., Růžičková L., Ryppl M., Ryšán M., Samek P., Schartner V., Svoboda M., Štoural J., Šimek L., Šipan J., Tyllner Z., Vaca D., Vlček J., Vogeltanz J., Vojtěch O., Vojtěchová Š., Vokurka M., Volfová J., Zahradka V. jun., Zach V., Zenáhlíková J., Zikmund O., Žemlička P., Žižka M. Special thanks for the information from the border area in Bavaria belong to the colleagues from the Bavarian Forest NP: Gahbauer M., Heurich M.

REFERENCES

- ANDĚL P., MINÁRIKOVÁ T. & ANDREAS M. (eds), 2010: *Ochrana průchodnosti krajiny pro velké savce* [Protection of permeability of landscape for the large mammals]. Evernia, Liberec, 137 pp. (in Czech with a summary in English).
- ANDĚRA M. & ČERVENÝ J., 2009: *Velcí savci v České republice. Rozšíření, historie a ochrana. 2. Šelmy (Carnivora)* [Large mammals in the Czech Republic. Distribution, History and Protection. 2. Carnivores (Carnivora)]. Národní Muzeum Praha, 215 pp. (in Czech with a summary in English).
- ANDĚRA M., ČERVENÝ J., BUFKA L., BARTOŠOVÁ D. & KOUBEK P., 2004: Současné rozšíření vlka obecného (*Canis lupus*) v České republice [Recent distribution of the wolf (*Canis lupus*) in the Czech Republic]. *Lynx, n.s.*, 35: 5–12 (in Czech with an English abstract).
- ANDĚRA M. & GAISLER J., 2019: *Savci České republiky: popis, rozšíření, ekologie, ochrana. 2. upravené vydání* [Mammals of the Czech Republic: Description, Distribution, Ecology and Protection, second, revised edition]. Academia, Praha, 286 pp. (in Czech with a summary in English).
- ANDRESKA J. & ANDRESKOVÁ E., 1993: *Tisíc let myslivosti* [Thousands years of game management]. Tina, Vimperk, 443 pp. (in Czech).
- BARTOŠOVÁ D., 2001: Současný výskyt a ochrana rysa ostrovida, medvěda hnědého a vlka na západním okraji Západních Karpat v CHKO Beskydy [Recent occurrence and conservation of eurasian lynx, brown bear and wolf at the western edge of the Western Carpathians, the Landscape protected area Beskydy]. *Chráněná území Slovenska*, 47: 14–17 (in Czech).
- BUFKA L., HEURICH M., ENGLEDER T., WÖFL M., ČERVENÝ J. & SCHERZINGER W., 2005: Wolf occurrence in the Czech-Bavarian-Austrian border region – review of the history and current status. *Silva Gabreta*, 11: 27–42.
- ČERVENÝ J., KOUBEK P. & BUFKA L., 2000: *Velké šelmy v naší přírodě* [Large carnivores in our nature]. Koršach, Praha, 32 pp. (in Czech).
- ČERVENÝ J., ANDĚRA M., KOUBEK P., HOMOLKA M. & TOMAN A., 2001: Recently expanding mammal species in the Czech Republic: distribution, abundance and legal status. *Beiträge zur Jagd-und Wildforschung*, 26: 111–125.

- ČERVENÝ J., ZIKMUND M. & FLÍČEK F., 2019: Wolf predation on ungulates and its impact on game management: case of Ralsko region, Northern Bohemia (Czech Republic). *Beiträge zur Jagd- und Wildforschung*, 44: 191–198.
- ČSÚ (Český statistický úřad), 2018: Hustota zalidnění [Human population density], online database. Online <https://reporting.uzis.cz/cr/index.php?pg=statisticke-vystupy--demograficke-a-socioeconomicke-ukazatele-pohyb-obyvatelstva-hustota-zalidneni-pocet-obyvatel-na-km2> (accessed on 9 June 2020) (in Czech).
- EEA (European Environmental Agency), 2017: EEA Reference Grid. Online <https://www.eea.europa.eu/data-and-maps/data/eea-reference-grids-2> (accessed on 21 March 2021).
- FEJKLOVÁ P., ČERVENÝ J., KOUBEK P., BARTOŠOVÁ D. & BUFKA L., 2004: Poznámky k potravě vlka obecného (*Canis lupus*) v České republice [Remarks to the food of the wolf (*Canis lupus*) in the Czech Republic]. *Lynx, n. s.*, 35: 27–33 (in Czech with an English abstract).
- FLOUSEK J., ZAJĄC T., KUTAL M., ŻUCZKOWSKI M., PALUCKI A., PUDIL M. & KAFKA P., 2014: Velké šelmy (Carnivora) v Krkonoších, Jizerských horách, Górach Stołowych a na Broumovsku [Large carnivores (Carnivora) in the Krkonoše Mts., Jizerské hory Mts., Góry Stołowe Mts. and the Broumovsko Region]. *Opera Corcontica*, 51: 37–59 (in the Czech with a summary in English).
- GULA R., 2008: Wolf depredation on domestic animals in the Polish Carpathian Mountains. *Journal of Wildlife Management*, 72: 283–289.
- HNUTÍ DUHA OLOMOUC, 2020: A wolf's journey from Austria to the Doupov Mountains. Online <http://www.carnivores.cz/articles/a-wolf-s-journey-from-austria-to-the-doupov-mountains/> (accessed on 31 March 2021).
- HULVA P., BOLFÍKOVÁ B.Č., WOZNICOVÁ V., JINDŘICHOVÁ M., BENEŠOVÁ M., MYSLAJEK R.W., NOWAK S., SZEWCZYK M., NIEDZWIECKA N., FIGURA M., HÁJKOVÁ A., SÁNDOR A.D., ZYKA V., ROMPORTL D., KUTAL M., FINÓ S. & ANTAL V., 2018: Wolves at the crossroad: Fission-fusion range biogeography in the Western Carpathians and Central Europe. *Diversity and Distribution*, 24: 179–192.
- HURKA L., 1981: Historie výskytu velkých šelem v západních a jihozápadních Čechách [The history of the occurrence of the large carnivores in the western and the south-western Bohemia]. *Zprávy Muzei Západočeského kraje, Příroda*, 24: 95–103 (in Czech).
- CHAPRON G., KACZENSKY P., LINNELL J.D.C., VON ARX M., HUBER D., ANDRÉN H., LÓPEZ-BAO J.V., ADAMEC M., ÁLVARES F., ANDERS O., BALČIAUSKAS L., BALYS V., BEDÓ P., BEGO F., BLANCO J.C., BREITENMOSER U., BRØSETH H., BUFKA L., BUNIKYTE R., CIUCCI P., DUTSOV A., ENGLEDER T., FUXJÄGER C., GROFF C., HOLMALA K., HOXHA B., ILIOPOULOS Y., IONESCU O., JEREMIĆ J., JERINA K., KLUTH G., KNAUER F., KOJOLA I., KOS I., KROFEL M., KUBALA J., KUNOVAC S., KUSAK J., KUTAL M., LIBERG O., MAJÍČ A., MÄNNIL P., MANZ R., MARBOUTIN E., MARUCCO F., MELOVSKI D., MERSINI K., MERTZANIS Y., MYSLAJEK R.W., NOWAK S., ODDEN J., OZOLINS J., PALOMERO G., PAUNOVIĆ M., PERSSON J., POTOČNÍK H., QUENETTE P.-Y., RAUER G., REINHARDT I., RIGG R., RYSER A., SALVATORI V., SKRBIŇSEK T., STOJANOV A., SWENSON J.E., SZEMETHY L., TRAJČE A., TSINGARSKA-SEDEFICHEVA E., VÁNA M., VEEROJA R., WABAKKEN P., WÖFL M., WÖFL S., ZIMMERMANN F., ZLATANOVA D. & BOITANI L., 2014: Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, 346: 1517–1519.
- JANÍK T., PETERS W., ŠÁLEK M., ROMPORTL D., JIRKŮ M., ENGLEDER T., ERNST M., NEUDERT J., HEURICH M., 2021: The declining occurrence of moose (*Alces alces*) at the southernmost edge of its range raise conservation concerns. *Ecology and Evolution*, 11: 1–16.
- KACZENSKY P., CHAPRON G., VON ARX M., HUBER D., ANDRÉN H. & LINNELL J.D.C., 2013: *Status, Management and Distribution of Large Carnivores – bear, lynx, wolf & wolverine – in Europe*. European Commission, Bruxelles, 72 pp.
- KOKES O., 1961: Šelmy v jižních Čechách a jejich konec [The carnivores in the southern Bohemia and their extirpation]. *Živa*, 9: 69–72 (in Czech).

- KUTAL M., ANDĚRA M., BARTONIČKA T., ČEPELKA L., SUCHOMEL J., DULA M. & ROMPORTL D., 2016a: *Výhodnocení počtosti a mezidruhových vazeb savců na území NP ČR a analýza vlivu a významu dotčených druhů a ekosystémy vyskytující se v zájmovém území* [The assessment of the abundance and interspecific relations of mammals on the territory of national parks in the Czech Republic and analysis of impact and importance of mammal species towards ecosystems in study areas]. Lesnická a dřevařská fakulta, Mendelova univerzita v Brně, Brno, 166 pp. (in Czech).
- KUTAL M., VÁŇA M., SUCHOMEL J., CHAPRON G., LÓPEZ-BAO J.V., 2016b: Trans-boundary edge effects in the Western Carpathians: the Influence of hunting on large carnivore occupancy. *Public Library of Science One*, 11: 1–15.
- KUTAL M., BELOTTI E., VOLFOVÁ J., MINÁRIKOVÁ T., BUFKA L., POLEDNÍK L., KROJEROVÁ J., BOJDA M., VÁŇA M., KUTALOVÁ L., BENEŠ J., FLOUSEK J., TOMÁŠEK V., KAFKA P., POLEDNÍKOVÁ K., POSPÍŠKOVÁ J., DEKAŘ P., MACHCINÍK B., KOUBEK P., DULA M., 2017: Výskyt velkých šelem – rysa ostrovida (*Lynx lynx*), vlka obecného (*Canis lupus*) a medvěda hnědého (*Ursus arctos*) – a kočky divoké (*Felis silvestris*) v České republice a na západním Slovensku v letech 2012–2016 (Carnivora) [Occurrence of large carnivores – *Lynx lynx*, *Canis lupus* and *Ursus arctos* – and of *Felis silvestris* in the Czech Republic and western Slovakia in 2012–2016 (Carnivora)]. *Lynx, n.s.*, 48: 93–107 (in Czech with a summary in English).
- LANDESIJÄGERSCHAFT NIEDERSACHSEN, 2021: Tabelle Totfunde Niedersachsen [Table of dead finds in Lower Saxony]. Online: https://www.wolfsmonitoring.com/fileadmin/dateien/wolfsmonitoring.com/Tabellen/Tabelle_Totfunde_.pdf (accessed on 25 March 2021) (in German).
- LANGHAMMER P., 1993: Habitatanalyse für den Wolf (*Canis lupus*) im Böhmerwald [Habitat analysis for the wolf (*Canis lupus*) in Bohemian Forest]. Ms., diploma thesis, Ludwig Maximilian Universität München, München, 100 pp. (depon. in the Šumava NP Administration, Kašperské Hory) (in German).
- LfU (Landesamt für Umwelt), 2017a: Männlicher Wolf im Nationalpark Bayerischer Wald stammt vermutlich aus der Alpenpopulation. Online <https://www.lfu.bayern.de/pressemitteilungen/archiv/l/757> (accessed on 19 March 2021) (in German).
- LfU (Landesamt für Umwelt), 2017b: Erster Nachweis von Jungwölfen im Bayerischen Wald. Online <https://www.lfu.bayern.de/pressemitteilungen/archiv/l/779> (accessed on the 25 March 2021) (in German).
- LINNELL, J.D.C., SMITH, M.E., ODDEN, J., KACZENSKY, P. & SWENSON, J.E., 1996: Strategies for the reduction of carnivore – livestock conflicts: a review. *Norwegian Institute for Nature Research Oppdragsmelding*, 443, 118 pp.
- MECH L.D. & BOITANI L. (eds), 2003: *Wolves: Behaviour, Ecology and Conservation*. The University of Chicago Press, Chicago, p. 1–448.
- MINÁRIKOVÁ T., POLEDNÍKOVÁ K., BUFKA L., BELOTTI E., ROMPORTL D., DIETZ S., PAVANELLO M., MUNNE S. & POLEDNÍK L., 2015: Výskyt středně velkých a velkých savců v jižních a jihozápadních Čechách (Carnivora, Artiodactyla, Lagomorpha) [Occurrence of medium-sized and large mammals in forests of southern and south-western Bohemia, Czech Republic (Carnivora, Artiodactyla, Lagomorpha)]. *Lynx, n.s.*, 46: 43–64.
- MZe (Ministerstvo zemědělství České republiky), 2019: Zpráva o stavu lesa a lesního hospodářství České republiky v roce 2018 [The report of the forest status and forest management in the Czech Republic in 2018]. Online <http://eagri.cz/public/web/mze/lesy/lesnictvi/zprava-o-stavu-lesa-a-lesniho-zprava-o-stavu-lesa-a-lesniho-4.html> (accessed on 9 June 2020) (in Czech).
- MOLINARI-JOBIN A., KÉRY M., MARBOUTIN E., MOLINARI P., KOREN I., FUXJÄGER C., BREITENMOSER-WÜRSTEN C., WÖFL S., FASEL M., KOS I., WÖFL M. & BREITENMOSER U., 2012: Monitoring in the presence of species misidentification: the case of the Eurasian lynx in the Alps. *Animal Conservation*, 15: 266–273.
- NABU (Naturschutzbund Deutschland), 2018: Wolfsrude aus dem Bayerischer Wald / Šumava schafft es nach Thüringen [The male wolf from the Bavarian Forest / Šumava makes it to Thuringia]. NABU,

- Berlin, press release. Online <https://thueringen.nabu.de/news/2018/24819.html> (accessed on 11 May 2019) (in German).
- NOWAK S., MYSLAJEK R.W., KLOSIŃSKA A. & GABRYŚ G., 2011: Diet and prey selection of wolves (*Canis lupus*) recolonising Western and Central Poland. *Mammalian Biology*, 76: 709–715.
- NOWAK S. & MYSLAJEK R.W., 2016: Wolf recovery and population dynamics in Western Poland, 2001–2012. *Mammal Research*, 61: 83–89.
- REINHARDT I., KLUTH G., NOWAK C., SZENTIKS C.A., KRONE O., ANSORGE H. & MUELLER T., 2019: Military training areas facilitate the recolonization of wolves in Germany. *Conservation Letters*, 12:e12635.
- ROMPORTL D. (ed.), 2017: *Atlas fragmentace a konektivity terestrických ekosystémů v České republice* [The atlas of fragmentation and connectivity of terrestrial ecosystems in the Czech Republic]. AOPK ČR, Praha, 30 pp. (in Czech).
- WEINGARTH K., HEIBL CH., KNAUER F., ZIMMERMANN F., BUFKA L. & HEURICH M., 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: 197–207.
- WEINGARTH K., ZEPPENFELD T., HEIBL CH., HEURICH M., BUFKA L., DANISZOVÁ K., MÜLLER J., 2015: Hide and seek: extended camera-trap session lengths and autumn provide best parameters for estimating lynx densities in mountainous areas. *Biodiversity and Conservation*, 24: 2935–2952.
- WWF, 2016: Isegrim ist zurück: Wolfsfamilie mit Jungtieren in Österreich gesichtet. Online <https://www.wwf.at/de/wolf-rueckkehr-allentsteig/> (accessed on 25 March 2021) (in German).

Received: 28 April 2021
Accepted: 20 August 2021