

Ungulate-vehicle crashes peak a month earlier than 38 years ago due to global warming

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Abstract

Global change has manifested itself as climate warming in Central Europe in recent decades. Average daily air temperatures increased by an average of 2 °C between 1982 and 2018. Air temperature changes have affected the timing of the vegetation periods (phenophases) and have also influenced the behaviour of animals. We worked with data on wildlife-vehicle crashes (WVC) recorded by the Czech Police in the period 1982–2019. Three peaks can usually be observed (spring, summer, and autumn) in the WVC time series. Eighty percent of these records involved roe deer (*Capreolus capreolus*). Such a high ratio allowed us to assume that any significant changes detected in WVC will be predominantly related to roe deer. We discovered that roe deer mortality on roads occurs earlier at present in the spring than in the past. The spring peak has shifted almost a month to the beginning of the year compared to the situation 38 years ago. The changes in the respective summer and autumn peaks were not statistically significant. The results suggest the effect of climate change on roe deer behaviour through increasing air temperatures and shifting vegetation phenophases. Thus, an earlier onset of deer activity associated with territory delineation and expected higher movement activity can be indirectly determined by the analysis of the WVC time series. The observed shift in the spring WVC peak in the roe deer model reveals a shift in ungulate behavioural patterns that is not evident from other biological data and thus surprisingly offers a suitable study framework for determining the impacts of environmental change on animals.

Keywords Wildlife · Wildlife-vehicle collisions · Phenophases · Ungulates · Central Europe

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1 Introduction

Climate change has manifested itself in most regions of Europe, among other ways, in the form of the average annual air temperatures (Hansen et al. 2010; EEA 2012). This increase in air temperature, observed since the 1980s, has affected vegetation, causing a shift in phenological phases (Schröder et al. 2014). Climate warming is increasingly disrupting natural phenological patterns, but the consequences of such disruptions for population dynamics and species interactions are poorly understood (Miller-Rushing et al. 2010; Forrest et al. 2016). The synchronisation of plant and animal life cycles with climate change is a long-established fact. It is well known, for example, that plant and animal life phenology is largely determined by the photoperiod and temperature. Together with the shifted phenology in plants, a shift in the life cycles of animals, that are directly dependent on vegetation, can also be expected. These may be not only herbivorous species but also species that depend on the vegetation in which they nest or forage. Climate warming poses two major challenges: exposure to higher temperatures and disruption of synchrony between juvenile rearing and resource emergence (Socolar et al. 2017). Rising temperatures, as a result of climate change, have led to an overall shift in the spring phenology of many organisms in the Northern Hemisphere (Menzel 2003; Schwartz 2006; Cleland et al. 2007; Roberts et al. 2015). The magnitude of this response could vary, however, among interacting species (Parmesan and Yohe 2003; Root et al. 2003). Phenological inconsistencies may therefore occur if a different magnitude of response disrupts previously synchronous trophic interactions (Visser et al. 1998; Koh et al. 2004).

1.1 Climate change and the behaviour of ungulates

Changes in direct climate variables, i.e. winter severity and snow depth, can affect ungulates via changes in plant phenology (Rickbeil et al. 2019), wildfire, invasive species, disease (Hoberg et al. 2008), and predation (Hebblewhite 2005). Moreover, changes in climate, vegetation, and food resources are accompanied by changes in circannual rhythms (Kappeler 2012). Behavioural changes in ungulates, due to climate change, have been already determined in several species, i.e. moose (Alces alces) where Jennewein et al. (2020) found that the impacts of climate change in arctic-boreal regions increase landscape heterogeneity through processes such as increased wildfire intensity and the annual area burned, which may significantly alter the thermal environment available to an animal; reindeer (Rangifer tarandus)—Paoli et al. (2020) stated that the plastic response of reindeer mating time to climatic variability demonstrated that environmental factors may have a significant influence on reproductive outputs; wild boar (Sus scrofa)—Touzot et al. (2020) in their study provided rare evidence that some species could greatly benefit from global warming thanks to higher food availability, in this case oak mast seeding on wild boar population dynamics. The impacts of the changing climate have also been documented with roe deer. The reason why climate change affects the roe deer phenophases is the availability and quality of food. Both are important factors for the use of space for game (Aikens et al. 2020, Jesmer et al. 2018; Bischof et al. 2012, Krop-Benesch 2013; Beck et al. 2006; Cook et al. 2004; Hebblewhite et al. 2008; Montgomery et al. 2013). High-quality forage enhances growth and the recruitment of migratory individuals (Bischof et al. 2012; Aikens et al. 2017). Plard et al. (2014) provided, however, a rare quantification of the demographic costs associated with the inability of roe deer to modify its phenology in response to the increasingly early onset of spring. Such a finding is in stark contrast to the pronounced phenotypic responses to climate change that have been observed in many other mammals.

1.2 Roe deer and wild boar annual cycles

Roe deer and wild boar are the most common ungulate species in Czech Republic. Their annual activity will be described below. Roe deer activity varies over the course of a year and is related to several distinct periods which differ between sexes and age (fawns, yearlings, and adults). Roe deer remain in winter groups over the first months of the year. The first important phase of roe deer activity begins during the spring (Reimoser 2012) and corresponds with the disintegration of winter groups and migration from winter to summer habitats (Stubbe 2008; Cagnacci et al. 2011; Steiner et al. 2014). The scattering of young individuals across the landscape (Etter et al. 2002) and the establishing of territories (Cagnacci et al. 2011; Reimoser 2012) is observed during the spring season. Males actively defend their territories during this period which precedes the rut (Liberg et al. 1998; Hoem et al. 2007; Johansson 2010). The second phase of high roe deer locomotory activity occurs at the turn of August. It is related to rutting season and therefore the high activity of males (Krop-Benesch 2013; Kämmerle et al. 2017). The third distinguished period of roe deer activity is observed at the turn of November and is related to clustering of animals into winter groups (up to 60 individuals, Mrlik 1998) usually formed in the open landscape and also mainly dependent on migration (Cagnacci et al. 2011).

Activity patterns of wild boar are biphasic or polyphasic, with high intraspecific variability during the season (Keuling et al. 2008); the main part of their activity is used for foraging. Wild boar are diurnal with small-scaled movements when undisturbed; this is assumed to be the natural behaviour (Briedermann 1971). They tend to become nocturnal and wide ranging under hunting pressure (Briedermann 1971). This is an obvious case of the behaviour of wild boar in the Czech Republic during the entire season. The rutting season regularly occurs in late autumn and early winter; however, reproduction can occur throughout the year (Kozdrowski and Dubiel 2004).

1.3 Central European ungulates and motor vehicle collisions

Concerning the fact that our research only focuses on the Central European landscape, we will focus on WVC with roe deer and wild boar exclusively. Roe deer are the species most frequently represented not only in Czech republic, but also in many wildlife-vehicle crash databases across Europe, e.g. in Hungary, Slovenia, Norway, and Sweden (Bíl et al. 2021). The large amount of this crash data has allowed for the detailed spatial and temporal analyses of roe deer—motor vehicle collisions. Concerning the temporal WVC data analyses, some studies have demonstrated the strong impacts of circannual and ultradian rhythms of roe deer on WVC daily and seasonal pattern (Groot-Bruiderink and Hazebroek 1996; Steiner et al. 2014; Kusta et al. 2017; Ignatavicius and Valskys 2017).

The long-term statistics of wildlife-vehicle collisions indicate that during the year, two or three main peaks in roe deer vehicle crashes can be observed in many European countries—spring, summer, and sometimes also an autumn peak (Steiner et al. 2014). These peaks in the number of WVC reflect both the spatial and activity pattern of roe deer behaviour. As mentioned previously, the spring peak corresponds to the creation of territories and is in all probability the result of the increased locomotory activity of roe deer (Cagnacci 2011; Stache et al. 2012). This fact of high activity of males during territory fights

was demonstrated by Krop-Benesch et al. (2013) who measured locomotory activity for 11 collared roe deer (6 males and 5 females) in National Park Bavarian Forest, Germany. They found that the highest number of "mean number of activity peaks per day" was detected in May. Males manifest, during this phase, high spatial behaviour as determined in a study from southern Sweden (Johansson 2010). This means that road crossing frequency can also be higher when males are defending their territories. Dal Compare et al. (2007) on their study from the eastern Italian Alps indicated that more males than females were killed during the spring (April and May) peak. Such information further supports the idea that this first peak reflects the higher male activity when defending their territories. A lack of experience by young individuals in crossing roads is likely also responsible for the high collision numbers during the spring (Madsen et al. 2002; Von Hoermann et al. 2020). The summer peak reflects the highest male activity during rutting (Kämmerle et al. 2017) and the last autumn peak is related to land use change and the gathering of animals into winter groups. The second highest number of WVC is that with wild boar, recently reaching up to 15% of all registered WVC (e.g. Bíl et al. 2017). WVC with wild boar has a typical pattern, completely different from that of roe deer, with only one pronounced maximum between October and November (Bíl et al. 2017; Bartonicka et al. 2018).

The aim of this work is to analyse a 38-year-long series of WVC in order to determine the stability of the WVC temporal pattern over a year. We specifically focused on the temporal stability of WVC peaks in order to determine their potential temporal shift which would indicate changes in ungulate behaviour due to global warming.

2 Data and methods

2.1 Data

2.1.1 WVC data

Data on WVC are available from two primary sources in the Czech Republic: police crash records and carcass and crash records from Srazenazver.cz, an animal-vehicle crash reporting application (Bíl et al. 2017). While police crash records only distinguish between a crash with a forest or a domestic animal, data in Srazenazver.cz also contains information on the species involved. We used this data to determine species proportions involved in WVC. The information on species was only available as of 2010. During that period (i.e. 2010–2020), roe deer was a dominant species involved in recorded WVC in Czech Republic. Its share on all WVC records oscillated between 75 and 85%, followed by wild boar (9–16%). WVC data also contained information about fallow deer (0.3–3.5%) and red deer (0.2–2.3%) (Bíl et al. 2017, 2021; Srazenazver.cz).

We also obtained hunting bag data from the unpublished reports of the Ministry of Agriculture (https://eagri.cz/public/web/mze/lesy/statistika/myslivost/x2011-2020/). Hunting bags data represents the most reliable, but indirect, information on population size.

We worked with a police crash database which contains 190,723 WVC recorded between 1982 and 2019 (Fig. 1). The overall rise in the number of WVC further reflects the expected increase in the population size of ungulates. The apparent drop in 2009 was caused by two factors: a change in WVC recording when only records above a certain limit were being recorded and two out of 13 Czech regions ended WVC registration in the police database.



2.1.2 Air temperature and DEM data

Daily maximum, minimum, and average air temperature data are publicly available data for 175 meteorological stations covering the entire Czech Republic (https://www.chmi.cz/ historicka-data/pocasi/denni-data/Denni-data-dle-z.-123-1998-Sb.) We further used digital elevation model (DEM) from Copernicus Land Monitoring Service (https://www.eea. europa.eu/data-and-maps/data/copernicus-land-monitoring-service-eu-dem.). DEM data were used to filter out meteorological data recorded at stations located at higher altitudes than the adjacent road network (e.g. from the highest part of the mountains).

2.1.3 Traffic volume data

The Road and Motorway Directorate of the Czech Republic maintains several hundred automatic traffic monitoring sites across Czech Republic, mostly at motorways and firstclass roads. The data are provided in the form of hourly sums representing traffic volume. The dataset is not publicly accessible but can be obtained for research purposes on request. Four sites with the longest time series (as of 2007) have been selected to represent changes in traffic volume. Two of them are at motorways (D1, 12th and 195th km) and the other two at first-class roads (I/3, 23rd km and I/43, 15th km).

2.2 Methods

2.2.1 WVC data analyses

Our aim was to determine possible temporal changes of WVC distribution over a year. All the computations were performed with the R software (R Core Team 2019). First, a general probability distribution over a year for the entire period was estimated with the use of the kernel density estimation (KDE; Silverman 1986; R routine "density"). Since the choice of a kernel function has only a minor effect on the resulting estimate (Bailey and Gatrell 1995), we used a default Gaussian kernel. The bandwidth was determined by the SJ method (Sheather and Jones 1991) which selects the optimal bandwidth using a pilot estimation of derivatives. Periodic boundary correction was also employed to obtain a

meaningful estimate in the boundary region, because the support of the probability density function is a bounded interval. This means that the same data points were virtually added before the first day and after the last day of the year.

Similarly, probability density functions for each particular year were estimated. In this estimation, there was no need to use the periodic boundary correction (with the exceptions of the years 1982 and 2019). Instead, data from three consecutive years were used to estimate the probability density function in the middle year.

Estimated probability density functions were also used to calculate quantiles of WVC as well as to determine local maxima of WVC occurrence. For both quantiles and local maxima, their trend over the period 1982–2019 was studied. In the first step, the Mann–Kendall trend test (Mann 1945; R package "Kendall"; McLeod 2011) was applied to determine if a monotone trend is present. Finally, a linear regression (Chambers 1992; R routine "lm") was used to evaluate the extent of the change if there was a statistically significant trend. When simultaneously performing multiple statistical tests, we employed the Bonferroni correction (Dunnett 1955). This means that the standard level of significance $\alpha = 0.05$ was substituted by α/n , where *n* stands for the number of simultaneously performed statistical tests.

2.2.2 Daily average air temperature data and GDD

To determine the minimum, maximum, and average daily air temperatures in the period 1982–2019, we categorised the area of Czech Republic according to altitude. The area of each altitude category was calculated. Then, based on the area, we randomly selected the proportionate number of meteorological stations, from which the air temperatures were used. This time series was then used to determine the cumulative growing degree days (GDD). GDD is a heuristic tool measuring heat accumulation. It is assumed that the relative growth of plants depends linearly on the cumulative GDD (Prentice et al. 1992; Ruml et al. 2010). GDD for a particular day can be approximately calculated as

$$\text{GDD} = \max\left(\frac{T_{\min} + T_{\max}}{2} - T_{\text{base}}, 0\right)$$

where T_{\min} and T_{\max} are daily minimum and maximum temperatures, respectively, and T_{base} is a base temperature. Cumulative GDD is calculated as a cumulative sum of GDD from the beginning of the year.

2.2.3 Traffic volume data analyses

Since time series of daily traffic volume contain missing data, a simple data imputation was performed prior to the analysis. Each missing value was substituted by a median of four values of the daily traffic volume: 2 weeks before, 1 week before, 1 week after, and 2 weeks after the particular day. If some of these values were also missing, they were excluded from the calculations (at least two values were available to estimate each single imputed value).

Similarly as for the WVC, quantiles of daily traffic volume over a year were calculated for each year within the period 2007–2019. The Mann–Kendall trend test was performed to evaluate whether there was a statistically significant trend. The Bonferroni correction for multiple comparisons was applied once again.

3 Results

A typical WVC pattern over a year can be observed from the estimated probability density function of WVC (Fig. 2). Apparently, there are three peaks (local maxima). The probability density function of WVC over a year varies in the period 1982–2019 (Fig. 3). It therefore makes sense to determine whether there are any trends in this variation.

First, we focused on the quantiles of the probability distribution of WVC. The reason was that WVC peaks were not always distinctive in data (see Fig. 3). The temporal change of quantiles was evaluated by the use of the Mann–Kendall test, which resulted in a statistically significant trend for 30% and 40% quantiles (on a level of significance accounting for 0.05/9 as 9 tests were performed simultaneously). Subsequently, linear regression confirmed that these two trends are decreasing, linear, and statistically significant (on the same level of significance). The extent of the decrease was 0.42 days per year and 0.49 days per year for 30% and 40% quantiles, respectively (Fig. 4).

Second, we focused on the peaks of the probability distribution of WVC. Their temporal changes were evaluated similarly as the temporal changes of quantiles (on the level of significance accounting for 0.05/3 as 3 tests were performed simultaneously). The Mann–Kendall test arrived at a statistically significant result only for the first (i.e. spring) peak. This result was confirmed by the use of the linear regression. The extent of the decrease was 0.75 days per year (27.75 days in total from 1982 to 2019). This means that the spring peak tends to occur 0.75 days earlier every year on average (Fig. 5).

Third, we examined the relationship between quantiles of WVC and the cumulative GDD. Since only 30% and 40% quantiles of WVC shifted towards the beginning of a year over the period in question, we were only interested in these two quantiles. Cumulative GDD was calculated for them while selecting two options for the base temperature: 5 °C and 10 °C. In neither case, was there a statistically significant trend (Mann–Kendall trend test, *p*-values: 0.9399 and 0.9599 for the 30% quantile, and 0.3145 and 0.6151 for the 40% quantile; Figs. 6 and 7).

As the last step, we focused on the quantiles of the traffic volume over a year (Fig. 8). In the period 2007–2019, no statistically significant trend was observed (Mann–Kendall trend test).

Fig. 2 Probability density function estimated by the use of the KDE method (Gaussian kernel with a bandwidth of 3.78 days determined by the SJ method and with periodic boundary correction). Source: WVC data 1980–2019, Czech Republic









Fig. 5 Temporal changes in the spring, summer, and autumn peaks on the number WVC in the period 1982–2019. The red colour highlights a statistically significant decreasing linear trend (*p*-value < 0.05/3, both Mann–Kendall test and linear regression) for the spring peak



Fig. 6 Temporal change of the cumulative GDD over the period 1982–2019 at dates of reaching the 30% quantile of WVC. The results for base temperatures of 5 °C and 10 °C are presented



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Fig. 8 Temporal change of quantiles of the traffic volume over a year at four selected sites (D1 motorway—two sites and I/3 and I/43 first class roads)

Description Springer

4 Discussion

We detected, on the basis of WVC data analysis, a temporal change of the first spring peak of WVC which currently occurs almost a month earlier than at the beginning of the time series under study (i.e. in 1982). We further determined that the cumulative GDD for the quantiles around the spring peak (i.e. 30 and 40%) has not changed over the entire period. This indicates that the spring peak of spring ungulate activity depends on temperature.

We further studied if changes in overall traffic would not be among the factors which could influence the observed peak shift. No statistically significant change in the quantiles of interest in traffic volume data for the four main roads and for a limited time series (as of 2007) has been observed.

As mentioned earlier, roe deer were the most frequently killed on roads. The problem is, however, that only data, related to species determination, are available as of 2010 onward. We therefore cannot explicitly claim that the detected shift of the spring WVC peak is only related to the roe deer as the ratio of the species was not available for older WVC records. There are, however, two indirect clues which allow us to assume that the WVC data from the beginning of the time series (here as of the 1980s) also represent roe deer as the most common species. The first one is related to official hunting bag data (Table 1).

Data on hunting bags is the only relevant information about the relative number of game animals in Czech Republic. It is evident that the ratio of roe deer was as high as 75% at the beginning of the study period, whereas the second highest numbers were those with wild boar and red deer (10%). The only important changes over the entire period were those related to the decrease of roe deer and the increase of wild boar, becoming thus the dominant animal in hunting bag statistics as of 2010 (45% vs. 38% for roe deer). We can assume that even when such a high representation of wild boar in hunting bags in recent years is only reflected in 15% share on WVC, this percentage can be expected to be even lower before 2010. Thus, only roe deer would remain as the most dominant species involved in WVC for the entire time series.

The second fact, supporting our hypothesis that the spring WVC peak reflects roe deer behaviour, is related to the time of this peak. While roe deer has its peak of locomotory activity and the related WVC peak during these spring months, WVC with wild boar are predominantly concentrated in the autumn and winter months.

4.1 Phenophase shift

As mentioned earlier, some authors, e.g. Pokorny (2006) and Rodríguez-Morales et al. (2013), have suggested that the prominent spring peak, which also occurs in WVC data in

	1980	%	1990	%	2000	%	2010	%	2020	%
Roe deer	84,846	0.75	86,757	0.48	112,795	0.51	119,838	0.38	101,494	0.30
Wild boar	11,773	0.10	55,812	0.31	67,858	0.31	143,378	0.45	155,561	0.46
Fallow deer	1877	0.02	5044	0.03	9413	0.04	14,113	0.04	30,333	0.09
Mouflon	2759	0.02	7580	0.04	7719	0.03	9050	0.03	10,480	0.03
Red deer	10,881	0.10	20,849	0.12	17,796	0.08	20,706	0.07	24,471	0.07
Sika deer	981	0.01	3156	0.02	5859	0.03	11,019	0.03	17,310	0.05
	113,117		179,198		221,440		318,104		339,649	

Table 1 Hunting bags for selected years covering the WVC time series under study

their countries (Slovenia and Spain), was related to pre-birth displacement of adult females, dispersal of yearlings, and, in particular, territorial behaviour of adult males. Similar peaks can also be seen across many European WVC data (Steiner et al. 2014).

The determined shift of the first WVC peak in this study thus indirectly indicates that the roe deer activity related to territory determination begins earlier than almost 40 years ago (Fig. 9). The main type of roe deer activity which moved to the beginning of year is thus in all probability related to territory defence and fighting of males. The secondary cause of this peak and consequently the influenced behaviour could be related to the dispersal of youngsters from last year (see Linnell et al. 1998).

4.2 Possible ecological impacts of the phenophase shift

Peak roe deer activity in March/April is related to the establishment of territories, while the peak of activity is during May/June with active defence of territories and rutting (Reimoser 2012). Some studies support that males actively defend a territory months ahead of the rutting (Liberg et al. 1998; Hoemet al. 2007; Johansson 2010). We consider rising air temperatures and overall spring phenology advancement for roe deer as having resulted in earlier active defence of territories, earlier increased spring locomotory activity (males and females), and thus an observed shift in the spring peak of vehicle accidents.

The activity of roe deer in the summer is mainly influenced by seasonal spermatogenesis and testosterone production (Blottner et al. 1996), while the autumn peak of activity is influenced by changes in landscape formation (Hewison et al. 1998; Cagnacci et al. 2011). As far as we know, the peak of the roe deer rut is not affected by global warming. Our results therefore suggest that climate change will lead to an increase in the period during which males actively defend their territories.



Climate change may also affect the timing of the dispersal of young animals across the landscape. There is a close association between a fawn and mother until it is 1 year old, and they disperse in late spring and early summer (Linnell et al. 1998; Van Moorter et al. 2008). There are no significant between-sex differences in dispersal rates (Linnell et al. 1998; Coulon et al. 2006). Due to global warming, there may be an earlier dispersion of young individuals of both sexes. This factor may also be the secondary explanation for the shift in the spring peak of vehicle accidents.

We can only speculate about the future character of the ecological impact of the observed change to the roe deer population. Shortening the period for establishing social hierarchy among males and, conversely, lengthening the period for defending territories can lead to changes in the structure of populations. Such changes may lead to adjustments in the management of the populations of this hunting important ungulate species. The negative impact of phenophase shift on roe deer has already been documented by Plard et al. (2014). They found, in their study from France's Champagne region, that grapevine flowering and spring vegetation start 2 weeks earlier than 27 years before due to global warming. This phenophase shift has a negative impact on roe deer as the average dates in which fawns were born did not change over the course of the study. They therefore documented the mismatch between the vegetation phase and the birth dates of the fawns. Decreased fawn survival is probably caused by the fact that females are unable to utilise the nutrition from the spring flush to provide their fawns with milk.

Recent climate change has significantly shifted the timing of major phenological events, such as the widely reported spring shift and autumn shift, involving even major crops (rice—Ye et al. 2019, Chen et al. 2021; corn—Hatfield and Dold 2018; cereals—Fu et al. 2014, Menzel et al. 2020) causing phenological mismatches across trophic levels including plants and ungulates (Renner and Zohner 2018). Roe deer in agricultural landscapes benefit significantly from higher metabolisable energy concentrations compared to forest environments (König et al. 2020), making the importance of phenophase shifts for their survival even more important.

4.3 The importance of WVC data for detection of climate change

This analysis indicated that the WVC data which is routinely gathered by the police, and which does not have any other aim than informing on traffic safety issues, can also be utilised for the determination of possible impacts of environmental factors on wildlife (specifically roe deer population). We therefore identified in this study the pronounced impact of climate change on the behaviour of the most widespread and most abundant ungulate, roe deer. This is also, to the best of our knowledge, the first work of this kind related to roe deer where determination of behavioural change was carried out using WVC data. Similar findings, i.e. the shift of the median dates of moose-vehicle collisions to the beginning of the year, were previously reported by Niemi et al. (2013) from Finland. Our study thus presents additional proof of the impact of climate change on ungulate behaviour in Europe.

The importance of this study also lies in the fact that usually no direct observation of changes in long-term roe deer behaviour is possible for the scale of the entire country. Although there are currently technologies, such as VHF or GPS collars (e.g. Kämmerle et al. 2017), available for precise monitoring of wildlife behaviour, only several up to tens of concurrently active collars are usually available (e.g. Bíl et al. 2020). Moreover, these techniques were not available several years ago and therefore state-wide data of this kind is missing. The WVC data thus can be used as surrogate data representing

roe deer seasonal activity and allowing for the determination of the eventual temporal changes in roe deer behaviour.

WVCs often also occur as a result of other causes than natural seasonal behaviour and related differences in ungulate locomotory activity. Taylor-Brown et al. (2019) and Plante et al. (2020), for example, reported a disturbance to wildlife by free-ranging dogs, cyclists in the field, or vehicles entering wildlife rest areas. In some groups of vertebrates, increased movement of tourists has also been associated with the large numbers of WVC (Garriga et al. 2012). Free-ranging dogs are a significant threat to wildlife (Taylor-Brown et al. 2019), with the disturbed individuals attempting to escape quickly and crossing roads in reduced vigilance. A similar situation can occur intentionally when wildlife is displaced and baited as part of joint hunts. These causes of WVC do not, however, occur in such a prominent temporal synchronicity as they are not directly related to the natural behaviour of roe deer.

5 Conclusion

Long-term climate warming in Central Europe can be demonstrated in the time series of air temperatures. Compared to the 1980s, an increase in mean annual temperature of almost 2 °C has been observed. This warming has further influenced the phenophases of plants and, consequently, animals. We assume that the determined change in the spring WVC peak is, in all probability, related to roe deer. Therefore, the roe deer activity, mainly related to active fighting and defence of territory, has been affected by climate change. This activity, evident in the shift in the spring peak of WVC, now begins almost a month earlier than 40 years ago. This work has shown that the long time series of WVC data currently available in many countries can also be used as surrogate data for assessing the effects of climate change on wildlife behaviour.

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Data availability Data is available from the corresponding author on request.

Declarations

Competing interests The authors declare no competing interests.

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References

- Aikens EO, Mysterud A, Merkle JA et al (2020) Wave-like patterns of plant phenology determine ungulate movement tactics. Curr Biol 30(17):3444-3449.e4
- Aikens EO, Kauffman MJ, Merkle JA, Dwinnell SP, Fralick GL, Monteith KL (2017) The greenscape shapes surfing of resource waves in a large migratory herbivore. Ecol Lett 20(6):741–750
- Bailey TC, Gatrell AC (1995) Interactive spatial data analysis. Longman, Essex, UK
- Bartonička T, Andrášik R, Duľa M, Sedoník J, Bíl M (2018) Identification of local factors causing clustering of animal-vehicle collisions. J Wildl Manag 82(5):940–947. https://doi.org/10.1002/jwmg. 21467
- Beck JL, Peek JM, Strand EK (2006) Estimates of elk summer range nutritional carrying capacity constrained by probabilities of habitat selection. J Wildlife Manage 70:283–294
- Bíl M, Andrášik R, Cícha V, Arnon A, Kruuse M, Langbein J, Náhlik A, Niemi M, Pokorny B, Colino-Rabanal VJ, Rolandsen CM, Seiler A (2021) COVID-19 related travel restrictions prevented numerous wildlife deaths on roads: a comparative analysis of results from 11 countries. Biol Conserv 256:109076
- Bíl M, Kušta T, Andrášik R, Cícha V, Brodská H, Ježek M, Keken Z (2020) No clear effect of odour repellents on roe deer behaviour in the vicinity of roads. Wildlife Biol 2020(4):wlb.00744. https://doi.org/ 10.2981/wlb.00744
- Bíl M, Kubeček J, Sedoník J, Andrášik R (2017) Srazenazver.cz: A system for evidence of animal-vehicle collisions along transportation networks. Biol Conserv 213:167–174. https://doi.org/10.1016/j.biocon. 2017.07.012
- Bischof R, Loe LE, Meisingset EL et al (2012) A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? Am Nat 180(4):407–24. https://doi.org/10.1086/667590
- Blottner S, Hingst O, Meyer HHD (1996) Seasonal spermatogenesis and testosterone production in roe deer (Capreolus capreolus). J Reprod Fertil 108(2):299–305. https://doi.org/10.1530/jrf.0.1080299
- Briedermann L (1971) Ermittlungen zur Aktivitätsperiodik des Mitteleuropäischen Wildschweines (Sus scrofa L.). Zool Gart 40:302–327
- Cagnacci F, Focardi S, Heurich M, Stache A, Hewison AJM, Morellet N, Kjellander P, Linnell JDC, Mysterud A, Neteler M, Delucchi L, Ossi F, Urbano F (2011) Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. Oikos 120:1790–1802. https://doi.org/10.1111/j.1600-0706.2011.19441.x
- Chambers JM (1992) Linear models. In: Chambers JM, Hastie TJ (eds.) Statistical models in S., 1st edn. Wadsworth & Brooks/Cole, pp 95-138
- Chen J, Liu Y, Zhou W, Zhang J, Pan T (2021) Effects of climate change and crop management on changes in rice phenology in China from 1981 to 2010. J Sci Food Agric 101:6311–6319. https://doi.org/10. 1002/jsfa.11300
- Cleland EE, Chuine I, Menzel A, Mooney HA, Schwartz MD (2007) Shifting plant phenology in response to global change. Trends Ecol Evol 22(7):357–365
- Cook RC, Cook JG, Mech LD (2004) Nutritional condition of northern Yellowstone elk. J Mammal 85:714–722
- Coulon A, Guillot G, Cosson JF, Angibault JMA, Aulagnier S, Cargnelutti B, Galan M, Hewison AJM (2006) Genetic structure is influenced by landscape features: empirical evidence from a roe deer population. Molecular Ecology 15(6):1669–1679. https://doi.org/10.1111/j.1365-294X.2006.02861.x
- Dal Compare L, Sturaro E, Cocca G, Ramanzin M (2007) An analysis of roe deer (Capreolus capreolus) traffic collisions in the Belluno province, eastern Italian Alps. Ital J Anim Sci 6(1):848–850
- Dunnett CW (1955) A multiple comparisons procedure for comparing several treatments with a control. J Am Stat Assoc 50(272):1096–1121. https://doi.org/10.1080/01621459.1955.10501294
- EEA (2012) Climate change, impacts and vulnerability in Europe 2012. European Environment Agency. https://www.eea.europa.eu/publications/climate-impacts-and-vulnerability-2012. Accessed 12 June 2023
- Etter DR, Hollis KM, Van Deelen TR, Ludwig DR, Chelsvig JE, Anchor CL, Warner RE (2002) Survival and movements of white-tailed deer in suburban Chicago, Illinois. J Wild Manag 66(2):500–510
- Forrest JR (2016) Complex responses of insect phenology to climate change. Curr Opin Insect Sci 17:49–54

- Fu YH, Piao S, Op de Beeck M, Cong N, Zhao H, Zhang Y, Menzel A, Janssens IA (2014) Multiscale observation of spring phenology. Glob Ecol Biogeogr 23:1255–1263. https://doi.org/10.1111/geb. 12210
- Garriga N, Santos X, Montori A et al (2012) Are protected areas truly protected? The impact of road traffic on vertebrate fauna. Biod Cons 21:2761–2774. https://doi.org/10.1007/s10531-012-0332-0
- Groot Bruinderink GWTA, Hazebroek E (1996) Ungulate traffic collisions in Europe. Conserv Biol 10(4):1059–1067
- Hansen J, Ruedy R, Sato M, Lo K (2010) Global surface temperature change. Rev Geophys 48:RG4004. https://doi.org/10.1029/2010RG000345
- Hatfield JL, Dold C (2018) Climate change impacts on corn phenology and productivity. In: Amanullah, Fahad S (eds) Corn production and human health in changing climate. London, UK: Intechopen. 95–114. https://doi.org/10.5772/intechopen.76933
- Hebblewhite M, Merrill E, McDermid G (2008) A multi-scale text of the forage maturation hypothesis in a partially migratory ungulate population. Ecol Monogr 78:141–166. https://doi.org/10.1890/06-1708.1
- Hewison AJM, Vincent JP, Reby D (1998) Social organisation of European roe deer. In: Andersen R, Duncan P, Linnell JDC (eds) The European roe deer: the biology of success. Scandinavian University Press, Oslo, Norway. pp. 189–219
- Hoberg EP, Polley L, Jenkins EJ, Kutz SJ (2008) Pathogens of domestic and free-ranging ungulates: global climate change in temperate to boreal latitudes across North America. Rev Sci Tech Oie 27(2):511–528
- Hoem SA, Melis C, Linnell JCD, Andersen R (2007) Fighting behaviour in territorial male roe deer Capreolus capreolus: the effects of antler size and residence. Eur J Wildlife Res 53:1–8. https://doi.org/10. 1007/s10344-006-0053-3
- Ignatavicius G, Valskys V (2017) The influence of time factors on the dynamics of roe deer collisions with vehicles. Landsc Ecol Eng 14:221–229
- Jennewein JS, Hebblewhite M, Mahoney P et al (2020) Behavioral modifications by a large-northern herbivore to mitigate warming conditions. Mov Ecol 8(39). https://doi.org/10.1186/s40462-020-00223-9
- Jesmer BR, Merkle JA, Goheen JR et al (2018) Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. Science 361(6404):1023–1025
- Johansson A (2010) Territory establishment and antler cycle in male roe deer. Ethology 102:549–559. https://doi.org/10.1111/j.1439-0310.1996.tb01147.x
- Kämmerle J-L, Brieger F, Kröschel M, Hagen R, Storch I, Suchant R (2017) Temporal patterns in road crossing behaviour in roe deer (*Capreolus capreolus*) at sites with wildlife warning reflectors. PLoS ONE 12(9):e0184761. https://doi.org/10.1371/journal.pone.0184761
- Kappeler P (2012) Verhaltensbiologie, Springer Spektrum, Göttingen
- Keuling O, Stier N, Roth M (2008) How does hunting influence activity and spatial usage in wild boar Sus scrofa L.? Eur J Wildl Res 54:729–737
- Koh LP, Dunn RR, Sodhi NS, Colwell RK, Proctor HC, Smith VS (2004) Species coextinctions and the biodiversity crisis. Science 305:1632–1634
- König A, Hudler M, Dahl S-A, Bolduan C, Brugger D, Windisch W (2020) Response of roe deer (Capreolus capreolus) to seasonal and local changes in dietary energy content and quality. Anim Prod Sci 60:1315–1325
- Kozdrowski R, Dubiel A (2004) Reproductive biology of wild boars. Vet Med-Sci Pract 60(12):1251–1253
- Krop-Benesch A, Berger A, Hofer H, Heurich M (2013) Long-term measurement of roe deer (*Capreolus capreolus*) (Mammalia: Cervidae) activity using two-axis accelerometers in GPS-collars. Ital J Zool 80(1):69–81. https://doi.org/10.1080/11250003.2012.725777
- Kusta T, Keken Z, Jezek M, Hola M, Smid P (2017) The effect of traffic intensity and animal activity on probability of ungulate-vehicle collisions in the Czech Republic. Safety Sci 91:105–113
- Liberg O, Johansson A, Andersen A, Linnel JDC (1998) Mating system, mating tactics and the function of male territoriality in roe deer. In: Andersen R et al (eds) The European roe deer: the biology of success. Scandinavian Univ, Press, pp 221–256
- Linnell JDC, Wahlstrom LK, Gaillard JM (1998) From birth to independence: birth, growth, neonatal mortality, hiding behaviour and dispersal In: Andersen R, Duncan P, Linnell JDC (eds). The European roe deer: the biology of success. Oslo: Scandinavian University Press, pp. 257–283
- Madsen AB, Strandgaard H, Prang A (2002) Factors causing traffic killings of roe deer Capreolus capreolus in Denmark. Wildlife Biol 8:55–61
- Mann HB (1945) Nonparametric tests against trend. Econometrica 13:245–259
- Menzel A (2003) Plant phenological anomalies in Germany and their relation to air temperature and NAO. Clim Chang 57(3):243–263
- Menzel A, Yuan Y, Matiu M et al (2020) Climate change fingerprints in recent European plant phenology. Glob Chang Biol 26:2599–2612. https://doi.org/10.1111/gcb.15000
- Miller-Rushing AJ, Høye TT, Inouye DW, Post E (2010) The effects of phenological mismatches on demography. Philos Trans R Soc Lond B Biol Sci 365:3177–3186

- Montgomery RA, Roloff GJ, Millspaugh JJ (2013) Variation in elk response to roads by season, sex, and road type. J Wildlife Manag 77(2):313–325
- Mrlik V (1998) Analysis of factors affecting the number of vigilant individuals in seasonal groups of roe deer. Folia Zool 47:13–19
- Niemi M, Tiilikainen R, Nummi P (2013) Moose–vehicle collisions occur earlier in warm springs. Acta Theriol 58:341–347. https://doi.org/10.1007/s13364-013-0151-z
- Paoli A, Weladji RB, Holand Ø, Kumpula J (2020) Response of reindeer mating time to climatic variability. BMC Ecol 20(44). https://doi.org/10.1186/s12898-020-00312-8
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42. https://doi.org/10.1038/nature01286
- Plante S, Dussault C, Richard JH, Garel M, Côté SD (2020) Untangling effects of human disturbance and natural factors on mortality risk of migratory caribou. Front Ecol Evol 8:154. https://doi.org/10.3389/ fevo.2020.00154
- Plard F, Gaillard J-M, Coulson T, Hewison AJM, Delorme D, Warnant C et al (2014) Mismatch between birth date and vegetation phenology slows the demography of roe deer. PLoS Biol 12(4):e1001828. https://doi.org/10.1371/journal.pbio.1001828
- Pokorny B (2006) Roe deer-vehicle collisions in Slovenia: situation, mitigation strategy and countermeasures. Vet Arh 76:177–187
- Prentice IC, Cramer W, Harrison SP, Leemans R, Monserud RA, Solomon AM (1992) A global biome model based on plant physiology and dominance, soil properties and climate. J Biogeogr 19:117–134
- R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/
- Reimoser S (2012) Influence of anthropogenic disturbances on activity, behavior and heart rate of roe deer (Capreolus capreolus) and red deer (Cervus elaphus), in context of their daily and yearly patterns. In: Cahler AA, Marsten JP (eds) Deer: habitat, behavior and conservation. Nova Science Publishers, Inc., pp 1–96
- Renner SS, Zohner CM (2018) Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. Ann Rev Ecol Evol Syst 49(1):165–182
- Rickbeil GJM, Merkle JA, Anderson G et al (2019) Plasticity in elk migration timing is a response to changing environmental conditions. Glob Change Biol 25:2368–2381. https://doi.org/10.1111/gcb.14629
- Roberts AMI, Tansey C, Smithers RJ, Phillimore AB (2015) Predicting a change in the order of spring phenology in temperate forests. Glob Change Biol 21(7):2603–2611
- Rodríguez-Morales B, Díaz-Varela ER, Marey-Pérez MF (2013) Spatiotemporal analysis of vehicle collisions involving wild boar and roe deer in NW Spain. Accid Anal Prev 60:121–133
- Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C et al (2003) Fingerprints of global warming on wild animals and plants. Nature 421:57–60
- Ruml M, Vuković A, Milatović D (2010) Evaluation of different methods for determining growing degree-day thresholds in apricot cultivars. Int J Biometeorol 54:411–422. https://doi.org/10.1007/ s00484-009-0292-6
- Schröder W, Schmidt G, Schönrock S (2014) Modelling and mapping of plant phenological stages as bio-meteorological indicators for climate change. Environ Sci Eur 26, 5. https://doi.org/10.1186/ 2190-4715-26-5
- Schwartz MD, Ahas R, Aasa A (2006) Onset of spring starting earlier across the Northern Hemisphere. Glob Chang Biol 12:343–351
- Sheather SJ, Jones MC (1991) A reliable data-based bandwidth selection method for kernel density estimation. J R Stat Soc B 53:683–690. http://www.jstor.org/stable/2345597
- Silverman BW (1986) Density Estimation. Chapman and Hall, London
- Socolar JB, Epanchin PN, Beissinger SR, Tingley MW (2017) Phenological shifts conserve thermal niches. P Natl Acad Sci 114(49):12976–12981. https://doi.org/10.1073/pnas.1705897114
- Stache A, Heller E, Hothorn T, Heurich M (2012) Activity pattern of European roe deer (Capreolus capreolus) are strongly influenced by individual behavior. Folia Zool 62:67–75
- Steiner W, Friedrich L, Hackländer K (2014) A review on the temporal pattern of deer- vehicle accidents: impact of seasonal, diurnal and lunar effects in cervids. Accid Anal Prev 66:168–181
- Stubbe C (2008) Rehwild: Biologie, Ökologie, Hege und Jagd. Kosmos, Stuttgart
- Taylor-Brown A, Booth R, Gillett A, Mealy E, Ogbourne SM, Polkinghorne A et al (2019) The impact of human activities on Australian wildlife. PLoS One 14(1):e0206958. https://doi.org/10.1371/journal. pone.0206958
- Touzot L, Schermer É, Venner S, Delzon S, Rousset C, Baubet É, Gaillard JM, Gamelon M (2020) How does increasing mast seeding frequency affect population dynamics of seed consumers? Wild boar as a case study. Ecol Appl 30(6):e02134. https://doi.org/10.1002/eap.2134

- Van Moorter B, Gaillard JM, Hewison AJM, Said S, Coulon A, Delorme D, WidmerO, Cargnelutti B (2008) Evidence for exploration behaviour in young roe deer (Capreolus capreolus) prior to dispersal. Ethology Ecology Evol 20:1–15. https://doi.org/10.1080/08927014.2008.9522539
- Visser ME, Noordwijk AJV, Tinbergen JM, Lessells CM (1998) Warmer springs lead to mistimed reproduction in great tits (Parus major). P Roy Soc Lond B Bio 265:1867–1870
- Von Hoermann C, Pagany R, Kirchner K, Dorner W, Heurich M, Storch I (2020) Predicting the risk of deer-vehicle collisions by inferring rules learnt from deer experience and movement patterns in the vicinity of roads. IEEE Conf Proc 10th Int Conf Adv Comput Inf Technol (ACIT), Freiburg pp 368– 373. https://doi.org/10.1109/ACIT49673.2020.9208843
- Ye T, Zong S, Kleidon A et al (2019) Impacts of climate warming, cultivar shifts, and phenological dates on rice growth period length in China after correction for seasonal shift effects. Clim Chang 155:127– 143. https://doi.org/10.1007/s10584-019-02450-5

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