Roadkill in a time of pandemic: the analysis of wildlife-vehicle collisions reveals the differential impact of COVID-19 lockdown over mammal assemblages

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Abstract

Collisions with vehicles are a major anthropogenic cause of mortality for wildlife, with conservation and evolutionary implications. Due to the COVID-19 pandemic, many countries worldwide enforced lockdowns which importantly reduced traffic, and therefore had unprecedented consequences for global wildlife populations.

We modeled how the two lockdown periods in spring and autumn 2020 influenced wildlife-vehicle collisions in Slovenia (central Europe), by comparing long-term (for the period 2010–2020) and high-quality time series data on road mortality of seven mammalian species: European roe deer (n = 53,259), red fox (n = 9,889), European badger (n = 5,170), brown hare (n = 5,050), stone marten (n = 4,267), wild boar (n = 1,188), and red deer (n = 1,088). We decomposed 2010–2019 data through autoregressive Bayesian Generalized Additive Models, and then we compared 2020 data to forecasts, aiming to estimate anomalies in number of collisions during both lockdown periods.

During the spring lockdown (16 March – 30 April 2020), we observed far less collisions than in the 2010–2019 average as well as in 2020 forecasts, for roe deer and badger. In the autumnal lockdown (20 October – 31 December 2020), we observed significantly less collisions for roe deer and wild boar. Traffic reduction in both lockdown periods had a major impact on roe deer, which in autumn and spring 2020 experienced 270–330 less road-related mortality cases than expected.

COVID-19 lockdown reduced traffic-related mortality for the majority of studied species. In some species, this decrease reached a magnitude of biological significance, which can have long-term repercussions on both evolution and management. Obviously, large-scale sanitary policies, imposing a reduction to human mobility, can have large-scale impacts on wildlife. As pandemics may increase in the next decades, we encourage further research exploring the consequences of their enforcement over global change and wildlife conservation and evolution.

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Introduction

The COVID-19 pandemic represents a major driver of global change and also a turning point for environmental conservation. Due to its dramatic effects on both human health and global economy[1], the pandemic has rapidly reshaped the political agenda, re-configuring the allocation of economic resources, with long-term consequences for climate and nature conservation policies that are still unclear and worrisome[2][3][4]. On the other hand, it also had several consequences for the environment and nature as well as their understanding by humans. Despite communication about SARS-CoV-2 spillover was haphazard[5][6], zoonoses received unprecedented attention. In turn, this gave traction to arguments in favor of reconciling economic growth with environmental and sanitary issues[7][8][9][10]. Moreover, sanitary measures tackling the spread of SARS-CoV-2 curtailed human movements worldwide[11], and forced billions of people to spend most of their time nearby home[12].

This created a unique large-scale field experiment to test for the effect of human mobility over the biosphere, especially wildlife[13], which showed both behavioral and numerical responses to decreased human pressures. At the behavioral level, many species increased their presence in anthropized environments[14], changed their daily rhythms of activity[15][16], and altered their foraging and migratory patterns[17][18]. At the demographic level, early evidences indicate that COVID-19 lockdowns decreased mortality through wildlife-vehicle collisions (WVC; in this paper used for collisions with lethal effect, i.e. the roadkill). For example, Bíl *et al*.[19] found that reduced traffic across 10 European countries and Israel, during spring 2020, decreased the overall road mortality by 19% in comparison with predictions based on 2015–2019 roadkills. Similar results were found by Shilling *et al*.[20] for 4 states in the United States, and by other studies at the local scale (e.g. amphibians and reptiles[16]; hedgehogs[21]; three marsupial herbivores[22]). However, all these studies employed pooled data from multiple species, mixtures of different datasets by their origin (e.g., police records, hunting statistics, observations of volunteers) or data about single species at the local scale, therefore not allowing to study the effect of COVID-19 related traffic reduction in more detailed ecological context.

Collisions with vehicles are an important global cause of wildlife mortality, which sometimes jeopardizes conservation efforts[23]. Assuming that susceptibility to collisions with vehicles partially depends upon individual traits critical for the adaptation to urban environments and man-made infrastructures, like boldness[24], WVC can exert long-term evolutionary pressures on wildlife populations in anthropized environments[25]. Due to these two aspects and altogether with preliminary evidences on the strong effect of COVID-19 countermeasures on roadkills[19][20][21][22], determining robust estimates about shifts in WVC during lockdown periods (LP) across multiple assembly of wildlife species is becoming paramount for obtaining a comprehensive picture about COVID-19 (but also traffic and changes in its volume) as a global driver of ecological change.

In this study, we aim to provide a first quantification of this kind, namely the first one considering species-specific effects in a set of multiple mammalian species, and encompassing both spring and autumn LP in 2020. Compared to existing studies, we relied on a large and reliable 11-years long dataset across a whole country (Slovenia), i.e. by using weekly numbers of WVC affecting 7 species of mammals, recorded through a standardized and robust scheme for monitoring wildlife mortality.

Methods

Study area, data collection and target species

The study was performed throughout Slovenia, a central European country covering a surface of 20,273 km^2, and characterized by a range of heterogeneous ecosystems located at the intersection of four major European geographical units: the Alps, the Mediterranean, the Pannonian Basin, and the Dinaric Alps.

Slovenia harbors among the most complex assemblages of mammals in Europe, which also include high densities of large ungulates and carnivores[26][27][28][29]. Due to the absence of large urbanized areas, a rich network of protected areas and a good environmental connectivity, these species live side-to-side with human throughout most of the country. This also results in negative human-wildlife interactions, including WVC. From a conservation viewpoint, WVC are a significant source of mortality for some large and medium-sized carnivores, such as the brown bear *Ursus arctos*[30] and the golden jackal *Canis aureus*[31][32], ungulates such as the roe deer *Capreolus capreolus*[33], and amphibians[34].

In order to improve population monitoring and management, the Hunters Association of Slovenia established in 2006 an on-line information system enabling also a systematic monitoring and archiving data on wildlife roadkills. Trained hunters are obliged to record roadkills for all game species and protected large mammals (by providing data on species, sex, estimated age for ungulates and large carnivores, date, and exact location of the collision) throughout the entire country. Collected data are then uploaded on a daily basis into the Central Slovene Hunting Information System[35]. The incentive for hunters to exactly report each roadkill lies in the fact that harvest plans in Slovenia are set for the total "elimination quotas" (i.e., hunting bags, plus all registered mortality regardless the causes), and hunting ground managers can be fined by 4,200 to 125,000 € when these quotas are not fulfilled. Therefore, hunters are highly motivated to find, remove, and register all road-killed individuals, as this helps them meeting their management objectives and avoiding fines. On the other hand, over-reporting is prevented by the fact that hunters have to collect, prepare and hand over relevant proofs on individuals that are found dead (e.g. left hemimandibles for all ungulates).

Considering the consistency of data during the whole study period (2010–2020), it is important that in Slovenia hunting is recognized as an important public service, therefore hunters were not restricted at all in their activities during the both COVID-19 lockdown periods (spring and autumn 2020). This ensured a constant detection effort of roadkills throughout the study period (also during LPs), allowing reliable comparison of 2020 data with previous years. However, to further minimize any risk of underreporting WVC due to restricted movement/activity of people in 2020,[19][20] we included data for all 415 non-professional hunting grounds managed by hunting clubs (average size of 4,500 ha), but we excluded data from 12 hunting grounds with special purposes (LPNs; approx. 10% of Slovene surface), managed by public institutions (Slovenia Forest Service and Triglav National Park). We excluded LPNs for the following reasons: (*i*) they are managed by public employees whose activity was affected during the LPs; (*ii*) most LPNs are very large (25,000–60,000 ha) and are in remote areas, therefore the percentage of undetected road-mortality cases could be higher; (*iii*) LPNs are in areas with a low density of roads, therefore the frequency of WVC in these hunting grounds is rather very low. As the proportion of roadkills in LPNs is very low, when considering the total national road mortality (for example, in 2019: 4.3% in roe deer, 2.6% in red fox (*Vulpes vulpes*), 4.7% in European badger (*Meles meles*), and 0.7% in wild boar, respectively), we can assume that the dataset used in this study reliably reflects the country-wide changes in WVC.

In this study, we extracted reports of registered roadkills of 7 species of mammals between 2010 and 2020: European roe deer (n = 53,259), red fox (*Vulpes vulpes*, n = 9,889), European badger (*Meles meles*, n = 5,170), brown hare (*Lepus europaeus*, n = 5,050), stone marten (*Martes foina*, n = 4,267), wild boar (*Sus scrofa*, n = 1,188), and red deer (*Cervus elaphus*, n = 1,088). These species were selected because they were those for which the highest number of collisions was reported, and because for majority of them annual peaks in traffic-related mortality both in Slovenia and Europe coincide either with the spring LP (roe deer[33][36][37][38][39]; badger[40][41][42]; red fox and stone marten[43]) or the autumnal LP (wild boar[38][44][45][46]; red deer[37][44]; red fox, stone marten and badger[43]). Moreover, as all these species have high capability of living in anthropized environments and even in urban areas [47] and are among the species the most often killed by traffic in Europe, as well as their seasonal and circadian activity rhythms strongly influence their exposure rates [36][37][43][44], they represent a valuable case study to explore the association between exceptional reduced volumes of traffic and associated changes in roadkills. Unfortunately, due to the low number of collisions (from only occasional to up to 30 per year per species), we were not able to model collision data for species of special conservation concern like European otter (*Lutra lutra*), brown bear, gray wolf (*Canis lupus*), golden jackal or the European lynx (*Lynx lynx*).

Data analysis

For each species, we aggregated roadkills on a weekly basis, then we decomposed time series by means of Bayesian Generalized Additive Models with: (*i*) a linear component, accounting for variation between years in the number of killed individuals, capturing long-term dynamics characterizing wildlife populations, (*ii*) a seasonal component, modeled as a B-spline, accounting for cyclical weekly fluctuations in the number of collisions, capturing seasonal changes in animal behavior increasing their movement rate and thus road crossings[48][49], periodic variations in traffic volume, or seasonal weather conditions affecting the safety of drivers (e.g. ice, fog), and (*iii*) an autoregressive component, to deal with temporal correlation between consecutive weeks. Each model was based on a Negative Binomial distribution of the error term. For each model we selected the optimal number of knots for the B-spline, and then we compared different autoregressive structures. Model selection was based on the Widely Applicable Information Criterion, the Deviance Information Criterion and the sum of log-converted Conditional Predictive Ordinal values, obtained from leave-one-out cross validation (CPO)[50][51]. To appreciate the effect of traffic reduction due to COVID-19 lockdowns over the number of WVC, we trained time-series model on 2010–2019 data. Then we compared weekly counts of WVC between 16 March and 30 April 2020 (spring LP), and between 20 October and 31 December 2020 (autumnal LP), with the predictive distribution obtained from our model. The predictive distribution represented the expected number of collisions in the various weeks of 2020, with its associated uncertainty, that we expected from our model trained on 2010–2019 data.

To quantify the overall impact of lockdown measures over the volume of collisions, we summed differences between observed and expected values. To increase transparency in this process, we adopted two different approaches, that could better highlight the importance of accounting for uncertainty in estimation. First, we calculated differences only for those weeks within lockdown periods, for which number of collisions lied outside of the 95% Bayesian Credibility Interval (hereinafter 95% CI) of the predictive distribution. These weeks were absolutely anomalous, showing a number of collisions that was higher or lower than any plausible value predicted by our model. We calculated differences between observed values and: (*i*) the median value from the predictive distribution, (*ii*) the closest bound of the 95% CI, (*iii*) the most distant bound of the 95% CI. These three differences represented three different scenarios, with different magnitudes in the number of collisions. As 95% CI are different from frequentist confidence interval[52], in the sense that not all values within them are equally plausible, differences with median values from the predictive distribution were the most plausible scenario, whereas differences with both bounds of the 95% CI were far less likely. Finally, as we also noted anomalies going beyond the lockdown periods, probably due to potential compensatory mechanisms (see the Discussion section), we also summed overall differences between observed weekly numbers of collisions and the median values from the predictive distribution throughout 2020. This second approach yielded an estimation for the entire 2020 effect on differences in species-specific collisions volume with respect to forecasts. We also generated a separate estimation of decreased road mortality for autumnal LP only, by comparing 2020 roadkills with the seasonal component of the time-series model for 2010–2019. This second comparison provided information on what would have happened in autumn 2020 in the case of the absence of any lockdown in spring 2020.

To better highlight changes that occurred in Slovenia following COVID-19 restrictions, we downloaded mobility data for the whole country from the Google COVID-19 Community Mobility Reports dataset (https://www.google.com/covid19/mobility/). These data represent the aggregated volume of daily movements of Google users who turned on their Location History setting, allowing Google to record their position, which is a default option for most smartphone devices using location apps such as GoogleMaps. For this study, we only considered movements to places that are traditionally reached by car, at least by some people: retail and recreation sites, parks and green areas, transit stations, and workplaces. To compare time-series, the relative index representing human movements was standardized and centered. Statistical analyses were carried out with the statistical software R[53] and INLA[54]. A complete overview of model selection and diagnostic checks is available in the Supplementary Information (**Appendix 1**).

Results

Model selection retained a model with a second-order autocorrelation structure for roe deer, a model without any temporal autocorrelation for the European badger and a model with a first-order autocorrelation structure for all the other species. We did not detect strong patterns in model residuals, nor against fitted values nor against covariates (**Appendix 1**). Models fitted 2010–2019 data quite well (Fig. 4, Supplementary Information). With the exception of red fox, whose number of roadkills markedly increased in 2019, the long-term component of our models had a small marginal effect over the number of collisions. There was relatively little variation among years (Fig. 5, Supplementary Information). Data about human mobility indicated a major reduction in most human movements across Slovenia in 2020, corresponding to the first (spring) and the second (autumnal) LP (Fig. 1, 2).

Species-specific differences between the observed and expected number of collisions in 2020 were heterogeneous (Fig. 1, 2; Table 1). In spring, the roe deer, European badger and stone marten expressed significantly less road mortality than expected, with most values not only being lower than the median of the posterior predictive distribution, but also falling outside of the 95% CI. Wild boar and red deer showed a similar pattern in roadkills for the autumn lockdown. We did not record any systematic discrepancy for red fox and brown hare roadkills in both periods. Moreover, we observed a mixture of weeks with less and more roadkills than expected for both the European badger and stone marten during the spring LP. The change in the number of collisions was particularly clear for roe deer. The most plausible decrease in road mortality of this species was between 270 and 330 individuals for the entire 2020, if we counted only weeks outside of the 95% CI or all observations, respectively (Table 1). In spring, the species suddenly experienced less collisions than expected, in correspondence to the start of the spring LP, at 16 March 2020. Then in summer roadkills of this species rapidly came back to the normal level, and numbers of killed individuals plummeted again after 20 October 2020, when the second LP was enforced. On the other hand, we observed a prolonged diminished number of roadkills of the European badger, for which road mortality remained low until October, but during the autumnal LP the roadkill of this species was higher than expected. On the contrary, red fox did not show any anomaly in roadkill numbers during both LPs but had road-related mortality below expectations during the summer.

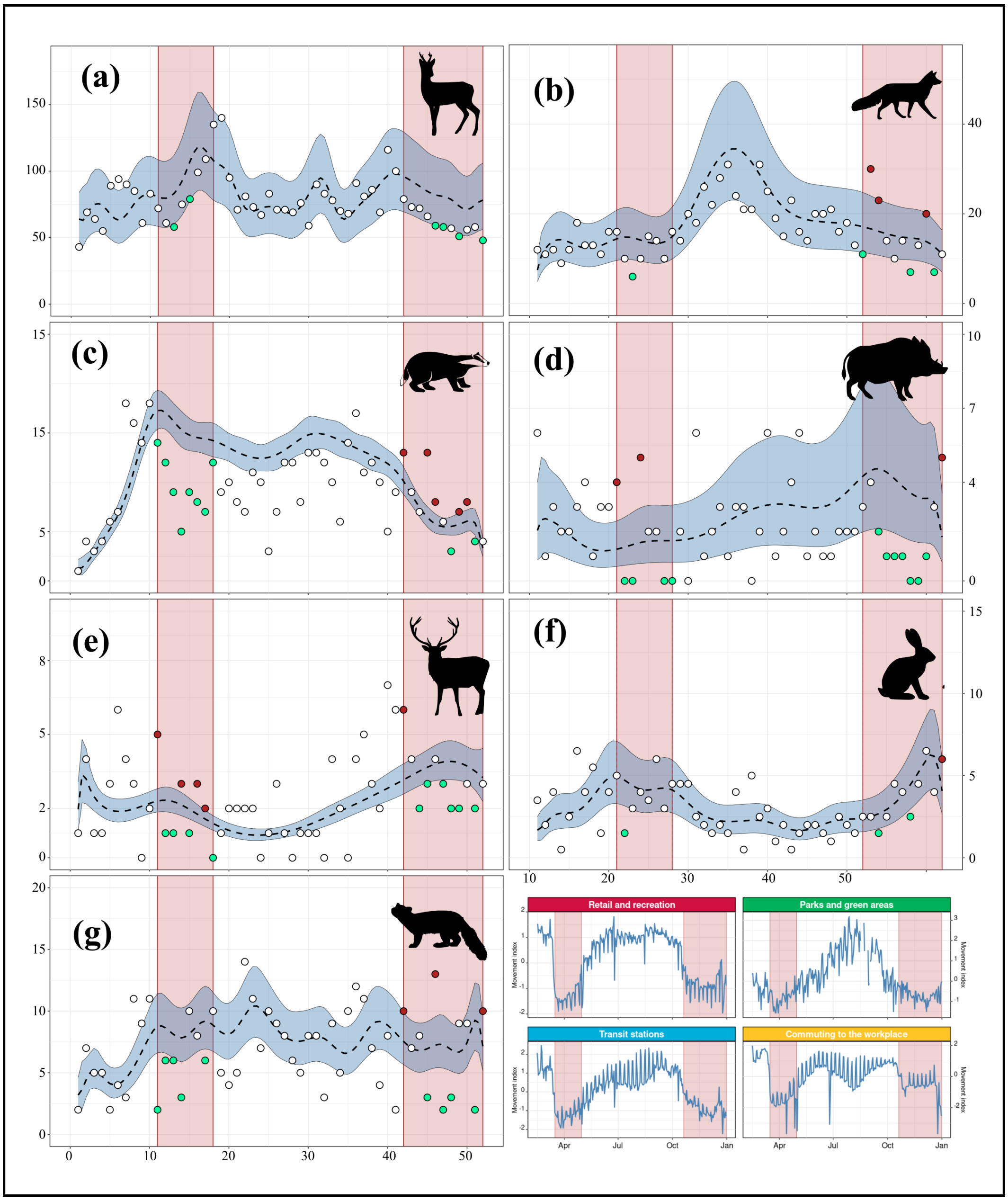

Figure 1: Comparison between 2020 observations, i.e. registered roadkills (points), and forecasts (modeled on 2010–2019 WVC dataset), for each species: a) *Capreolus capreolus*, b) *Vulpes vulpes*, c) *Meles meles*, d) *Sus scrofa*, e) *Cervus elaphus*, f) *Lepus europaeus*, g) *Martes foina*. Shaded rectangles represent the first and the second lockdown periods (LP), in March–May and October–December 2020. Green and red dots represent 2020 observations exceeding the 95% CI of the predicted values. In the lower-right corner of the Figure is an overview about variation in the daily volume of four types of human mobility in 2020, extracted from Google (darker areas represent LPs).

Discussion

To the best of our knowledge, this is the first study considering the potential effects of COVID-19 lockdown, and its consequent reduction in vehicular traffic, on WVC across multiple mammal species, and over an entire country. Aiming to do this, we compared 2020 roadkills with robust predictions about expected roadkills per each of seven mammals by using high-quality data from the previous decade. Data were collected through a nation-wide standardized protocol for reporting roadkills of large and medium sized mammals with the help of hunters, who can be important citizen scientists in the field of wildlife monitoring[55]. These are major advances of our research in comparison with similar studies, where several species with different ecological characteristics were pooled together and where data were obtained using different, non-standardized approaches/sources[19][20], or where predictions were generated from data with a shorter timespan or collected at the local scale[16][21][22].

Based on our findings, we can affirm that strong reductions in human mobility, and therefore in vehicular traffic density, due to sanitary measures against COVID-19 had the potential to affect wildlife populations through a reduction in road mortality. However, the magnitude of this effect was not homogeneous across wildlife species, varying in function of biological characteristics, like breeding phenology. This suggests that a widespread reduction in human mobility is likely to produce heterogeneous effects on wildlife assemblages and that COVID-19 has the potential to affect not only wildlife populations but also indirectly the ecosystems where they live in, by changing the magnitude and the temporal distribution of WVC. For example, in the case of roe deer, road mortality in 2020 was clearly curtailed and the magnitude of this phenomenon was around 270–330 animals during the whole year. Considering that in Slovenia between 4,500 and 5,900 roe deer die in collisions each year, representing 11.0–14.2% of the total registered mortality[56], our results correspond to a 4.5–7.3% reduction in expected yearly roadkills.

Such a reduction might not seem very important, at a first glance. However, roadkills are not homogeneous in space but rather clustered in hotspots, mostly around urbanized areas, and in the eastern, low-altitude part of the country (Fig. 3). In these areas, the proportion of roadkills in the total registered mortality of roe deer is much higher (15–20% on the district level (>100,000 ha large), and even >30% in some hunting grounds (in average: 4,500 ha)), and it is probably concentrated on individuals with specific personality traits[57], and/or on specific demographic categories with higher dispersal potential such as male yearlings[33][37]. Therefore, at these smaller scales, relaxing mortality by a several dozens of individuals per year is likely to be biologically important as they would (in a normal year) have not reproduced and spread their genes and personality otherwise. For example, in some deer species bolder individuals, while better at exploiting urbanized areas, are also probably more prone to traffic-related mortality[25]. With a reduction in the risk of collisions, their presence in a population can increase through time, hence influencing population demography and related characteristics, such as spatial and reproductive behavior.

At a superficial glance, this aspect might seem to be of a secondary importance, because COVID-19 lockdowns were limited in time. Nonetheless, once we consider the global scale of the pandemic, and how our findings are generalizable to various species and countries, we can imagine how COVID-19 LPs could have affected the selection of behavioral traits in wildlife living in anthropized environments worldwide[58]. A moderate selective pressure, applied across vast spatial scales, can have significant implications for global evolutionary dynamics of wildlife. Also, it is plausible that restrictions to human mobility will help counteracting future pandemics and also SARS-CoV-2, in case it becomes endemic[59]: which pressures will be exerted, in the long run, if local lockdowns occur on a regular basis? We believe that such questions are absolutely relevant, and should be investigated more into details also by considering that many species of wildlife are already subjected to specific management practices acting on their personality traits[25][60][61].

Our findings also clearly indicate that not all species were affected by reduction in human mobility at the same way, and that species-specific characteristics, such as the circadian rhythm of activity and breeding phenology[48][49], importantly moderated changes in road mortality in 2020. For example, wild boar and red deer experienced a slight decrease in their roadkills between October and December, during their breeding and post-breeding periods when individuals increase their movements[62] or are more subjected to increased anthropogenic pressures due to autumnal recreational activities in forests and intensive drive hunts[46]. On the other hand, species with multiple mating periods, such as the European badger, showed complex patterns in their reduction of road mortality, with partially compensatory dynamics. For example, badgers recorded very low road mortality in spring 2020, which continued into summer. However, the number of road-killed individuals then increased and became anomalously high in autumn, during the second LP. Badgers are mostly nocturnal and are a polyestrous species: they can mate at any time of the year, but the main peak occurs in spring (between February and May), and may be followed by a second in autumn, involving either females that have not previously been fertilized or those that have experienced superfetation[63][64][65]. Consequently, this species typically exhibits two peaks in traffic collisions, in spring and fall[41]. When a night-time

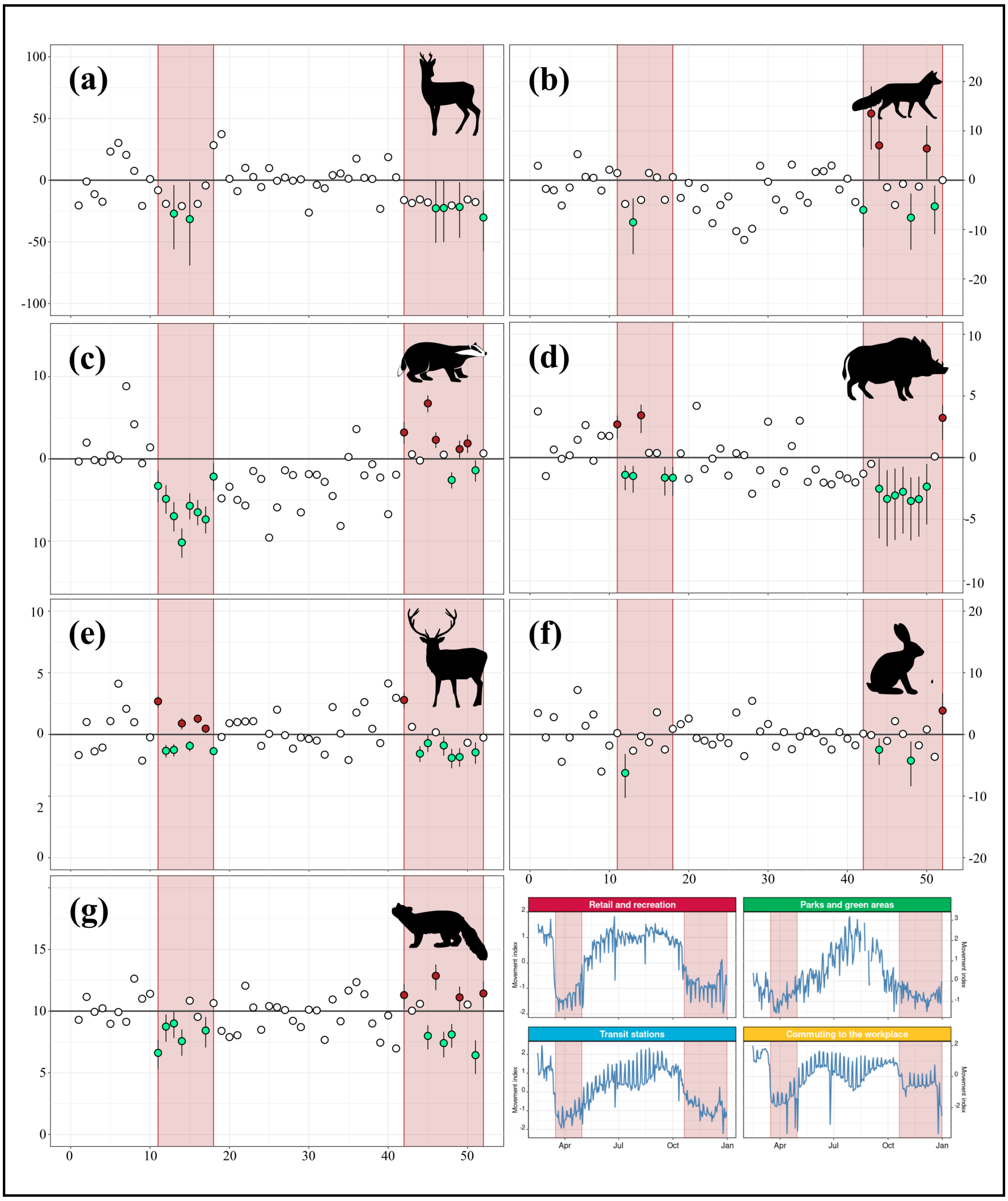

Figure 2: Differences between 2020 observations (i.e., registered roadkills) and forecasts (modeled on 2010–2019 WVC dataset), for each species: a) *Capreolus capreolus*, b) *Vulpes vulpes*, c) *Meles meles*, d) *Sus scrofa*, e) *Cervus elaphus*, f) *Lepus europaeus*, g) *Martes foina*. Points refer to differences between observations and median predicted values, vertical bars refer to comparison with the nearest and the farthest bound of the 95% CI. Shaded rectangles represent the first and the second lockdown periods (LP), in March–May and October–December 2020. Green and red dots represent observations exceeding the 95% CI of the predicted values. In the lower-right corner of the Figure is an overview about variation in the daily volume of four types of human mobility in 2020, extracted from Google (darker areas represent LPs).

curfew was imposed in spring LP in 2020, there was very low traffic mortality in badgers, particularly adults, which also increased offspring survival, population size and the pool of unfertilised females. Then, in autumn, several demographic and/or behavioral responses probably overlapped to increase the number of collisions: (*i*) high numbers of surviving juveniles started to move/disperse, (*ii*) many adult individuals not killed in spring, and probably more unfertilised females, made the second mating season more intense than usual, (*iii*) possible behavioral changes due to lower traffic density could also occur (i.e., badgers came closer to roads and crossed them more frequently).

Such of a species-specific heterogeneity in changes of WVC during 2020 LPs indicates that responses of mammal assemblages to large-scale reductions in human mobility due to COVID-19 are more pronounced and complex than previously thought. While for some species there are some clear demographic (and potentially also evolutionary) implications, for others the scenario is far less clear. This raises questions about trophic cascades: if some species are more affected than others, did trophic networks change their structure, following COVID-19 pandemic? And in case this change was significant, were ecosystem affected? Other perturbation experiments, like the removal of invasive alien species from the environment[66], or mass mortality events, indicated that trophic cascades can take often unforeseen directions because of the differential reactions of various species to the perturbation, often with negative consequences for the functionality of entire ecosystems[67]. Considering that in many environments there are species highly susceptible to collisions, whose numerical reduction can rapidly trigger trophic cascades[68][69], it would be important to understand whether the reduction in human mobility following COVID-19 pandemic also had consequences over trophic webs and cascade dynamics.

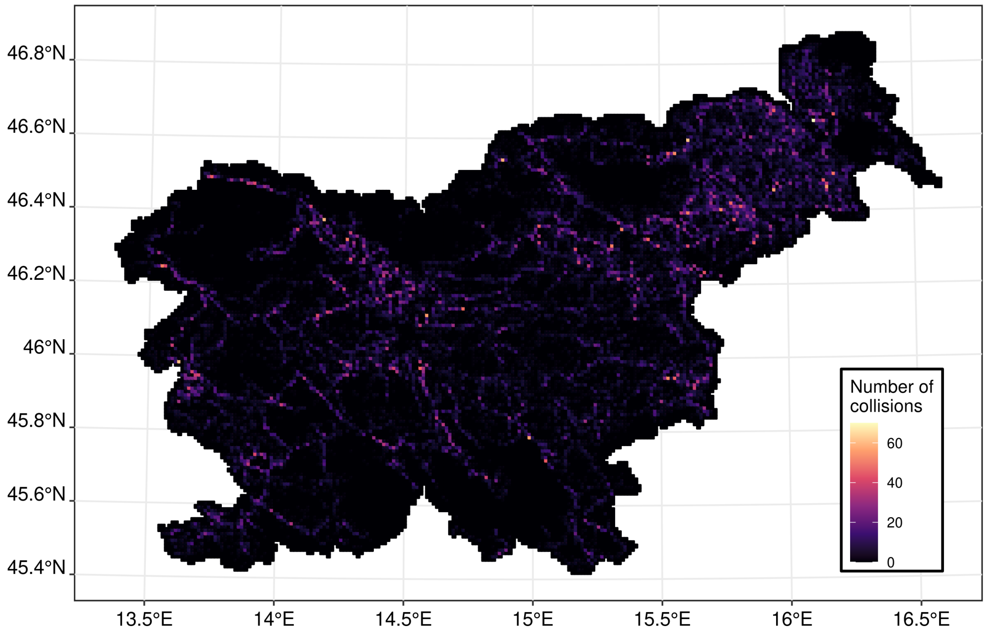

Figure 3: Map of the density of road mortality of roe deer in Slovenia, between 2010 and 2020, cumulated over a 1x1 km grid. Areas without roadkill are darker, whereas hotspots are highlighted in bright colors.

Conclusion

This study constitutes a first attempt to evaluate, in a robust and accurate way, the reduction in road mortality across different mammals due to the reduction in human mobility and vehicular traffic, that followed the implementation of COVID-19 lockdowns in 2020.

Our findings indicate that a temporally limited, but intensive and widespread, reduction in traffic had variable effects on the number of WVC across wildlife species, and for some of them, the ones the most vulnerable to collide with vehicles, the decreased volume of collisions can be substantial. However, the magnitude of the decrease and its seasonal pattern throughout 2020 seem to be strongly influenced by ecological and behavioral characteristics of each species, which should be considered either in activities for reducing the number of WVC or when using this number as an index of change in species abundance, i.e. for the scope of adaptive population management. Considering that the reduction in human mobility due to COVID-19 is a global phenomenon, and that wildlife communities worldwide include species with different susceptibility to collisions, we believe that our findings are generalizable to many countries, in all of their main messages.

By reducing the number of wildlife-vehicle collisions, the epidemiological health measures against COVID-19 disease can also affect populations' demography and dynamics, wildlife communities, and possibly their evolution as well as ecosystem functioning. Considering that this pandemic is far from being solved, from now on we need to carefully evaluate all these aspects, and their implications, in conservation biology.

Table 1. Estimated differences between observed (in 2020) and forecasted (modeled on 2010–2019 dataset) roadkill's of the seven species of mammals. "Spring 2020" and "Autumn 2020" refer to lockdown periods (LP) in 2020 (spring LP: 16 March – 30 April; autumnal LP: 20 October – 31 December), while "Entire 2020" refers to the whole duration of the year, also including weeks outside LPs. "Observations outside of 95% CI" refer to the sum of differences between observations outside the 95% Bayesian credibility Interval of forecasted values, while "All observations" consider data within and outside of the 95% CI. "Expected values" refers to the sum of differences between observed data and the median value of the predictive posterior distribution of our model, the value with the highest level of plausibility. "Closest boundary 95% CI" refers to the sum of differences between observed data and the closest boundary of the 95% CI, while "Furthest boundary 95%CI" refers to the sum of differences between observed data and the opposite boundary of the 95% CI. It must be emphasized that boundaries of the 95% CI have the lowest level of plausibility, among forecasted values.

	Spring 2020				**Autumn 2020**				**Entire 2020**
	Observations outside 95%CI			**All observations**	**Observations outside 95%CI**			**All observations**	**All observations**
	Expected values	**Closest boundary 95%CI**	**Furthest boundary 95%CI**	**Expected values**	**Expected values**	**Closest boundary 95%CI**	**Furthest boundary 95%CI**	**Expected values**	**Expected values**
C. capreolus	-59	-5	-126	-102	-97	-10	-207	-219	-270
V. vulpes	-9	-4	-15	-17	+8	+2	+4	0	-91
S. scrofa	0	+1	-4	+1	-18	-5	-41	-19	-19
M. meles	-47	-34	-61	-47	+11	+8	+14	+13	-96
C. elaphus	0	0	0	0	-6	-2	-10	-6	+10
L. europaeus	-6	-3	-10	-8	-3	-2	-7	-6	-12
M. foina	-19	-9	-32	-17	-9	-8	-13	-14	-34

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Acknowledgments

We would like to express our thanks to Hunters Association of Slovenia for developing systematic monitoring of WVC in Slovenia, and implementing an on-line hunting information system enabling us to access the comprehensive dataset on roadkills of studied species.

Funding

This study was funded by: (*i*) the Slovenian Research Agency (project V4–1825 and V1–2031, programme groups P4–0107 and P1–0386, and the Open Access publication fee); (*ii*) the Ministry of Agriculture, Forestry and Food of the Republic of Slovenia (both above mentioned projects); and (*iii*) the STEP CHANGE European Union's Horizon 2020 Research and Innovation Program under grant agreement No. 101006386, oriented to accelerate collaboration of hunters as citizen scientists in wildlife/biodiversity monitoring and research.

Author's contribution

Conceptualization: B.P., J.C. and E.B.; data management and providing: B.P.; statistical analyses: J.C.; writing – draft preparation: J.C.; writing – review and editing: B.P. and E.B.; funding: B.P. and E.B. All authors have read and agreed to the published version of the manuscript.

Dataset and reproducible software code

The dataset, altogether with the reproducible software code, are available on the Open Science Framework repository, at the following link: **https://osf.io/ak3vt/**

Supplementary Figures and Tables

Table S1. Estimated differences between observed (in 2020) and the seasonal component of the 2010–2019 time-series about roadkills of the seven species of mammals. “Spring 2020” and “Autumn 2020” refer to lockdown periods (LP) in 2020 (spring LP: 16 March – 30 April; autumnal LP: 20 October – 31 December),while "Entire 2020" refers to the whole duration of the year, also including weeks outside LPs. “Observations outside of 95% CI” refer to the sum of differences between observations outside the 95% Bayesian Credibility Interval of the seasonal component, while “All observations” consider data within and outside of the 95% CI. “Expected values” refers to refers to the sum of differences between observed data and the closest boundary of the 95% CI, while “Furthest boundary 95% CI” refers to the sum of differences between observed data and the opposite boundary of the 95% CI. Boundaries of the 95% CI have the lowest level of plausibility, among predicted values.

	Spring 2020				**Autumn 2020**				**Entire 2020**
	Observations outside 95%CI			**All observations**	**Observations outside 95%CI**			**All observations**	**All observations**
	Expected values	**Closest boundary 95%CI**	**Furthest boundary 95%CI**	**Expected values**	**Expected values**	**Closest boundary 95%CI**	**Furthest boundary 95%CI**	**Expected values**	**Expected values**
C. capreolus	-194	-41	-386	-225	-359	-76	-712	-359	-932
V. vulpes	-8	-3	-14	-11	+18	+8	+21	+8	-40
S. scrofa	+2	+2	-1	-3	-10	-2	-24	-11	+7
M. meles	-25	-18	-32	-24	+26	+19	+32	+26	+11
C. elaphus	+3	+3	+3	+3	+1	+2	0	+1	+29
L. europaeus	-32	-12	-58	-39	-35	-13	-64	-46	-158
M. foina	-20	-10	-32	-18	-8	-9	-9	-6	-39

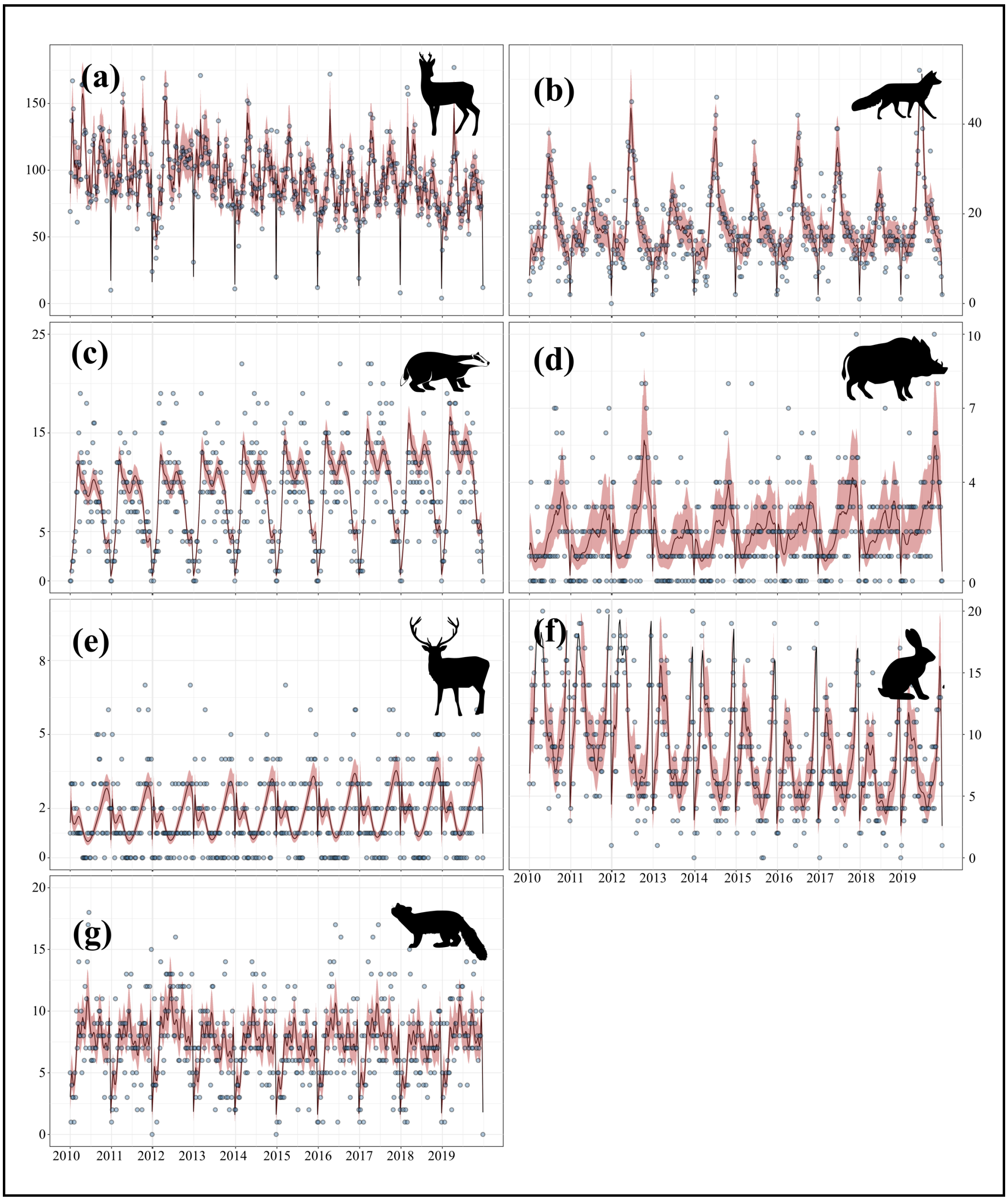

Figure S1: Fitted values for 2010–2019 and weekly number of roadkill: a) *Capreolus capreolus*, b) *Vulpes vulpes*, c) *Meles meles*, d) *Sus scrofa*, e) *Cervus elaphus*, f) *Lepus europaeus*, g) *Martes foina*.

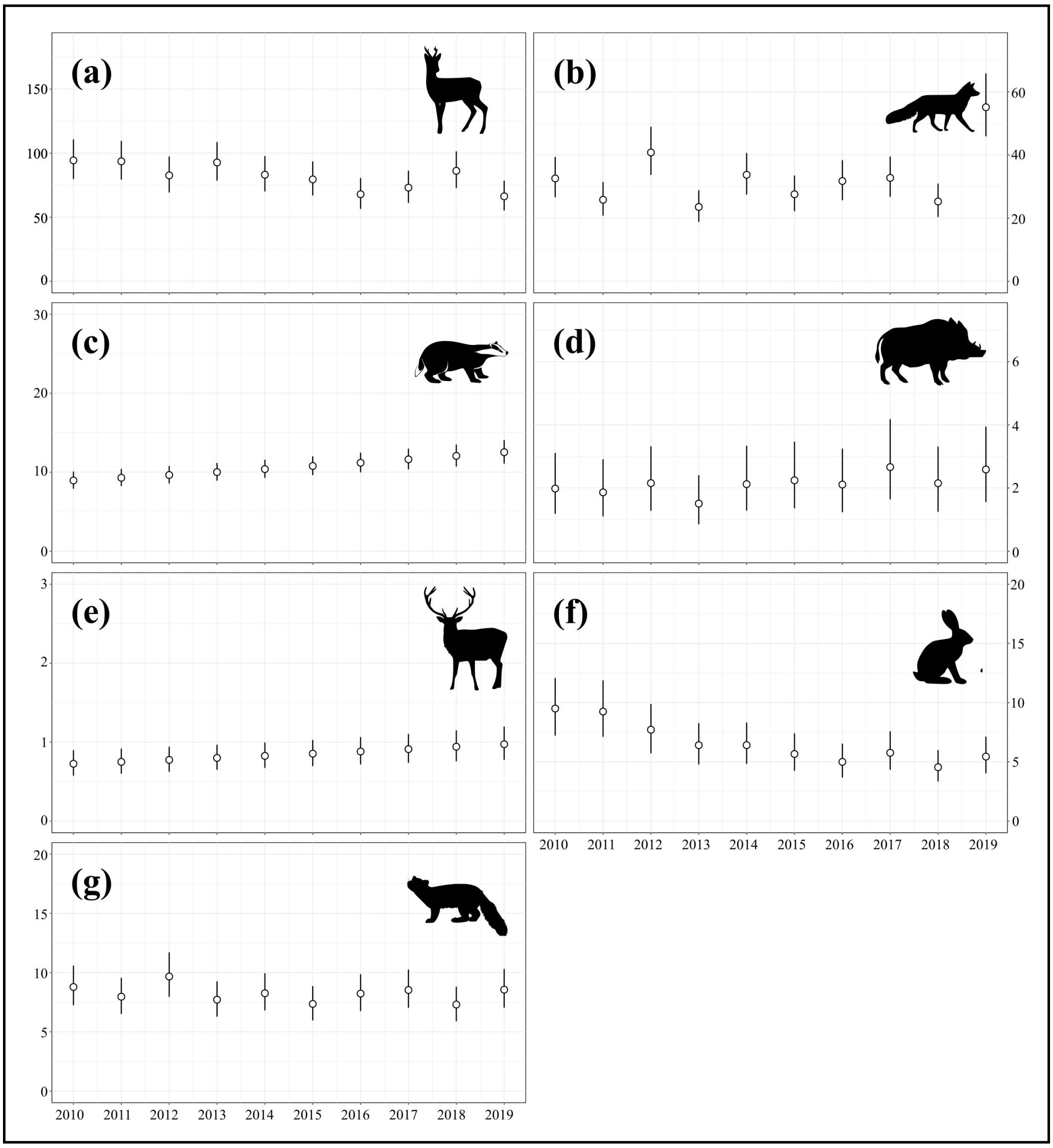

Figure S2: Long-term trends in the roadkill of seven studied species, variation between years: a) *Capreolus capreolus*, b) *Vulpes vulpes*, c) *Meles meles*, d) *Sus scrofa*, e) *Cervus elaphus*, f) *Lepus europaeus*, g) *Martes foina*. Vertical bars represent 95% CI around the marginal effect.

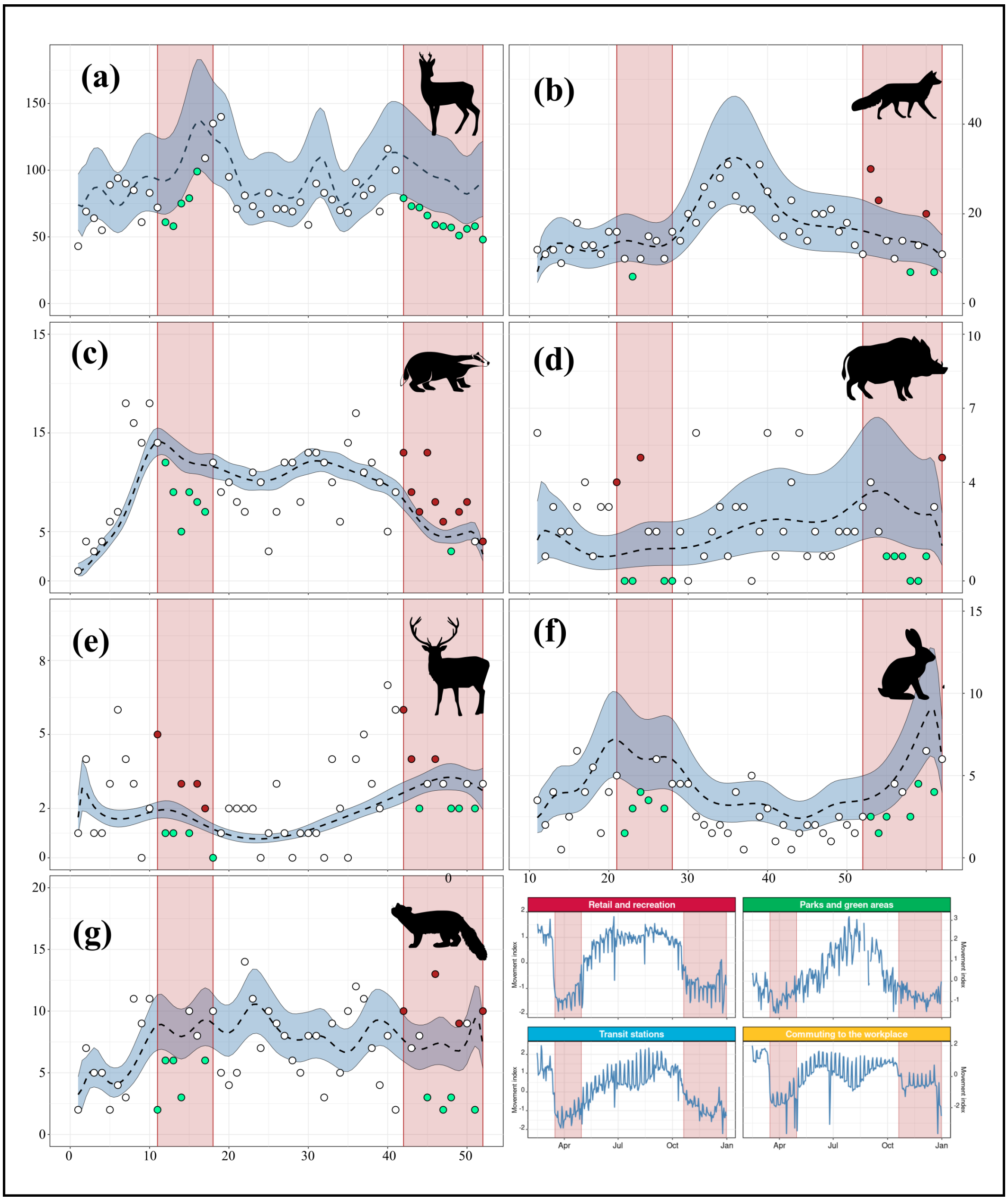

Figure S3: Comparison between 2020 observations, i.e. registered roadkill (points), and the seasonal component of the time series (2010–2019), for each species: a) *Capreolus capreolus*, b) *Vulpes vulpes*, c) *Meles meles*, d) *Sus scrofa*, e) *Cervus elaphus*, f) *Lepus europaeus*, g) *Martes foina*. Shaded rectangles represent the first and the second lockdown periods (LP), in March–May and October–December 2020. Green and red dots represent 2020 observations exceeding the 95% CI for the seasonal component of 2010–2019 period. In the lower-right corner of the Figure is an overview about variation in the daily volume of four types of human mobility in 2020, extracted from Google (darker areas represent LPs).

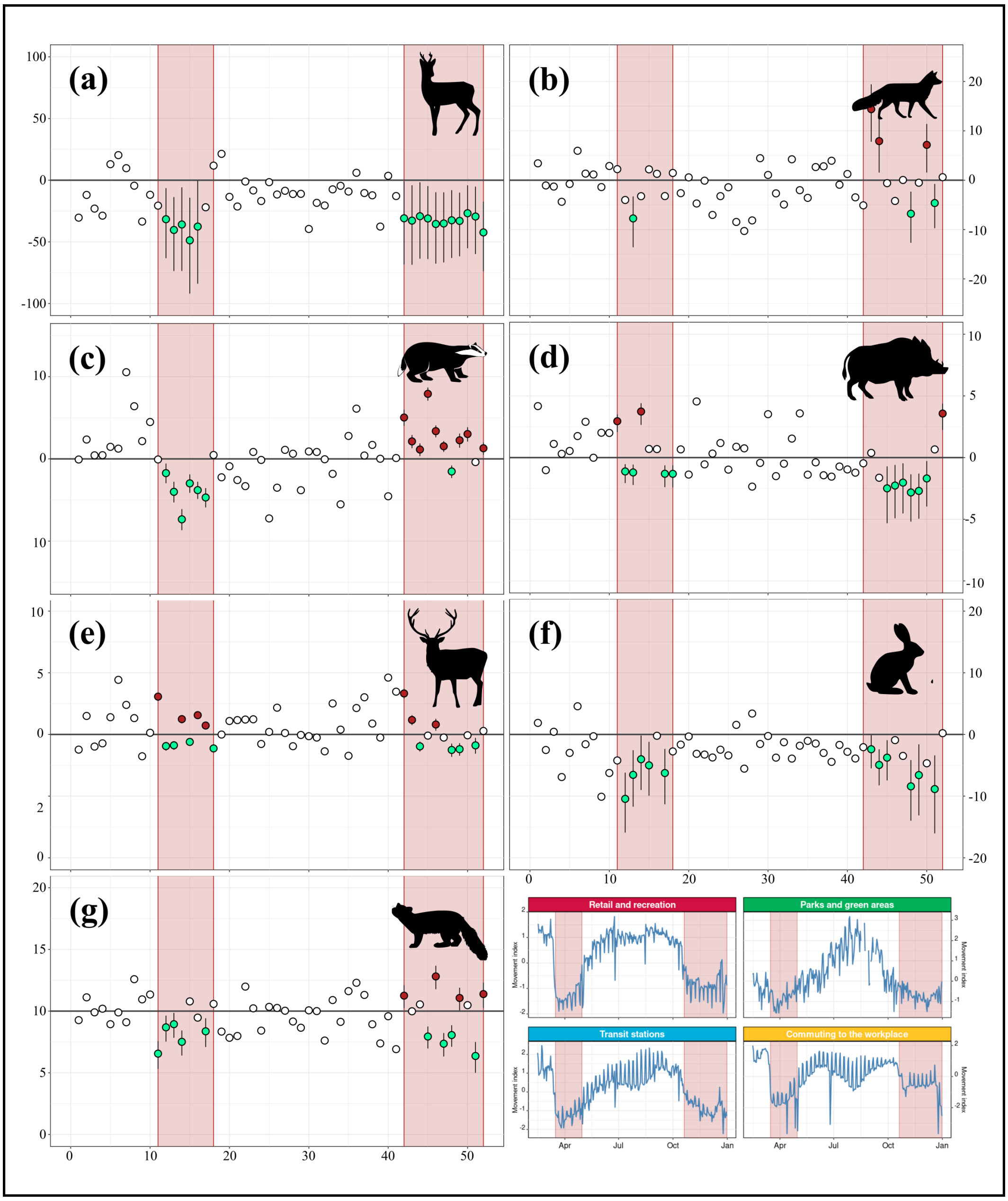

Figure S4: Differences between 2020 observations (i.e., registered roadkills) and fthe seasonal component of the time series (2010-2019), for each species: a) *Capreolus capreolus*, b) *Vulpes vulpes*, c) *Meles meles*, d) *Sus scrofa*, e) *Cervus elaphus*, f) *Lepus europaeus*, g) *Martes foina*. Points refer to differences between observations and median predicted values, vertical bars refer to comparison with the nearest and the farthest bound of the 95% CI. Shaded rectangles represent the first and the second lockdown periods (LP), in March–May and October–December 2020. Green and red dots represent 2020 observations exceeding the 95% CI for the seasonal component of 2010–2019 period. In the lower-right corner of the Figure is an overview about variation in the daily volume of four types of human mobility in 2020, extracted from Google (darker areas represent LPs).

Appendix 1

In the following lines, the main outputs of each model are shown. These are: (*i*) comparison between Generalized Additive Models with different autocorrelation structures for their residual error terms, (*ii*) the lag between residuals, (*iii*) the scatterplot of fitted values of each model versus its residuals, (*iv*) the scatterplot of model residuals versus covariates[50][51].

Roe deer (*Capreolus capreolus*)

Model	**WAIC**	**DIC**	**CPO**
No AR structure	4534.1	4527.4	-2267.3
AR1	4347.3	4336.4	-2192.9
AR2*	4302.8	4304.6	-2193.1
AR3	4339.3	4336.8	-2192.8

Table A - Comparison between the starting model and models with a 1st, 2nd and 3rd order autoregressive structure, accounting for temporal correlation. Indexes: Widely Applicable Information Criterion (WAIC), Deviance Information Criterion (DIC) and sum of log-converted Conditional Predictive Ordinal values (CPO). The best candidate model is highlighted.

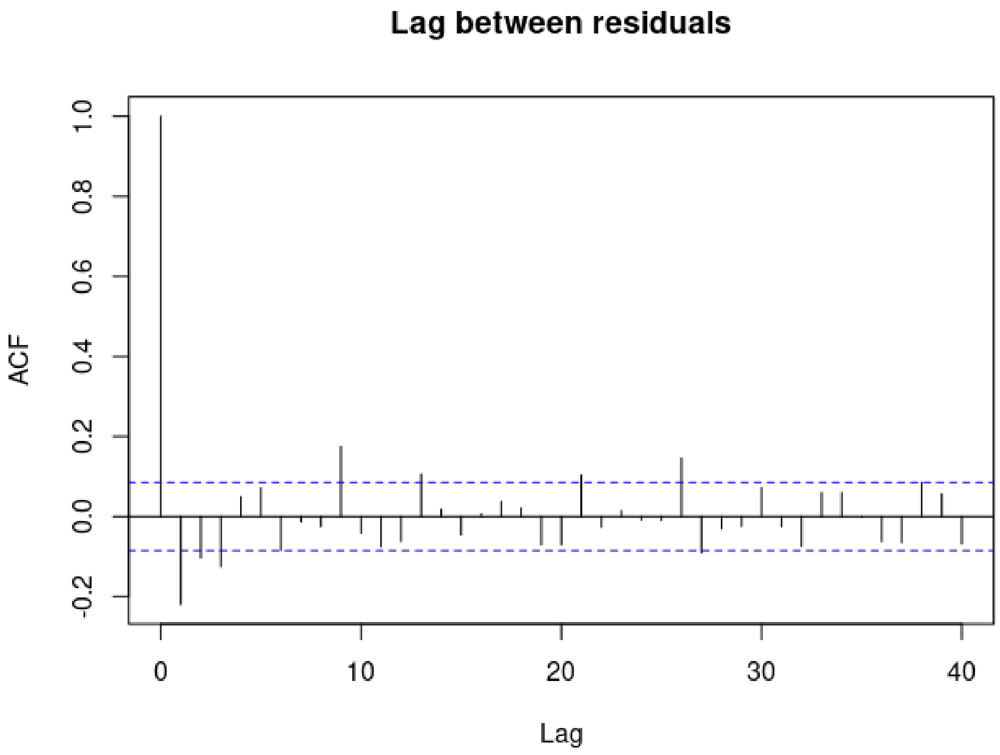

Figure A1: Roe deer: temporal lag between model residuals of the AR2 model.

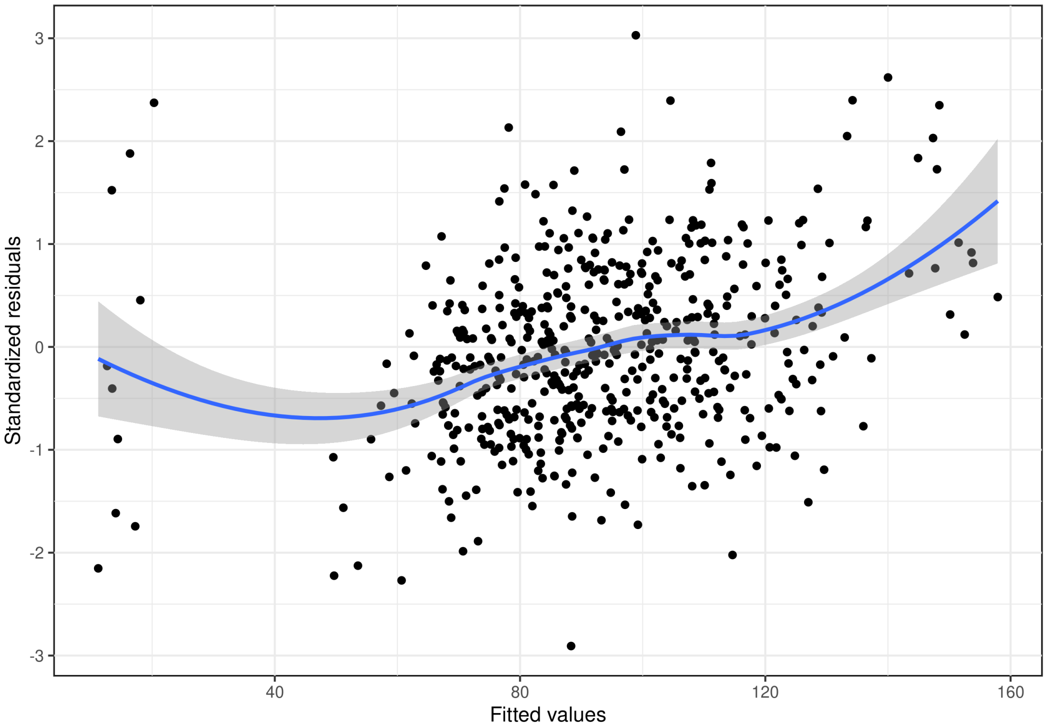

Figure A2: Roe deer: residuals versus fitted values of the AR2 model.

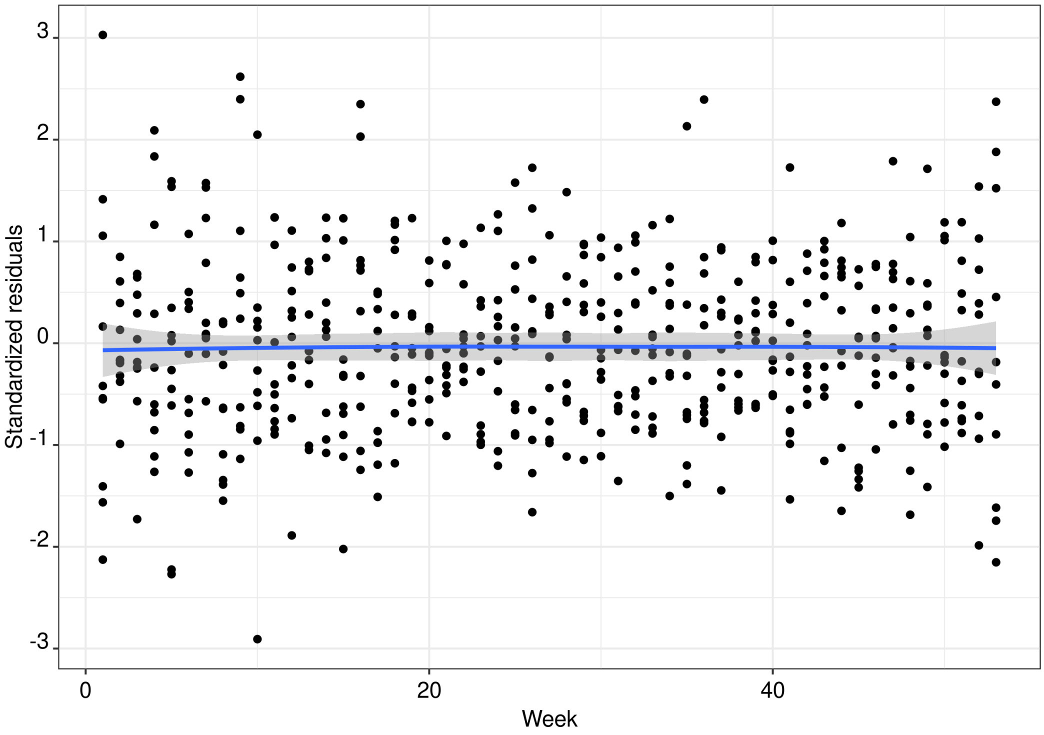

Figure A2: Roe deer: residuals versus the weekly term of the AR2 model.

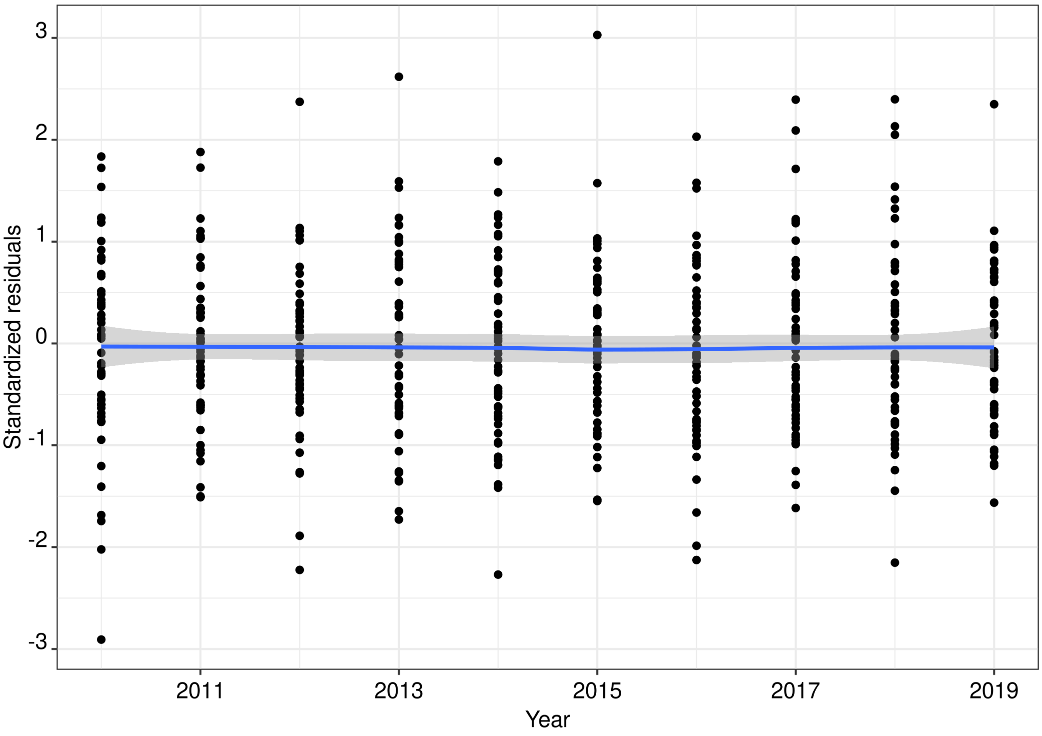

Figure A4: Roe deer: residuals versus the yearly term of the AR2 model.

Red fox (*Vulpes vulpes*)

Model	**WAIC**	**DIC**	**CPO**
No AR structure	3217.9	3216.9	-1608.9
AR1[*]	3101.8	3097.2	-1555.1
AR2	3100.2	3096.4	-1555.3
AR3	3100.6	3098.9	-1555.9

Table B - Comparison between the starting model and models with a 1st, 2nd and 3rd order autoregressive structure, accounting for temporal correlation. Indexes: Widely Applicable Information Criterion (WAIC), Deviance Information Criterion (DIC) and sum of log-converted Conditional Predictive Ordinal values (CPO). The best candidate model is highlighted.

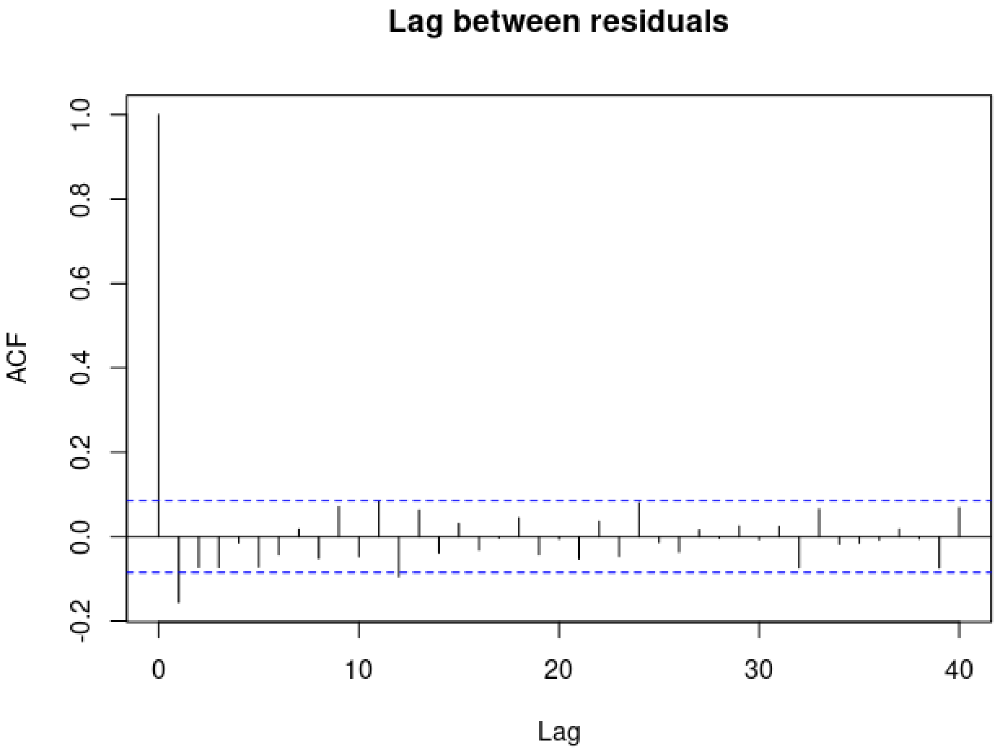

Figure B1: Red fox: temporal lag between model residuals of the AR1 model.

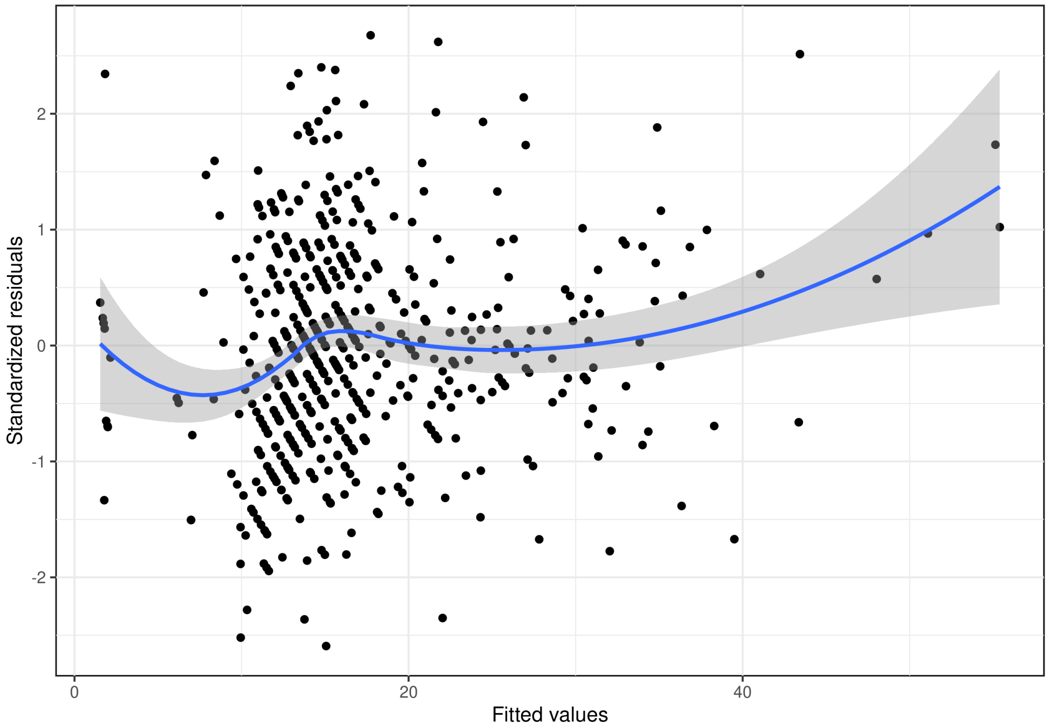

Figure B2: Red fox: residuals versus fitted values of the AR1 model.

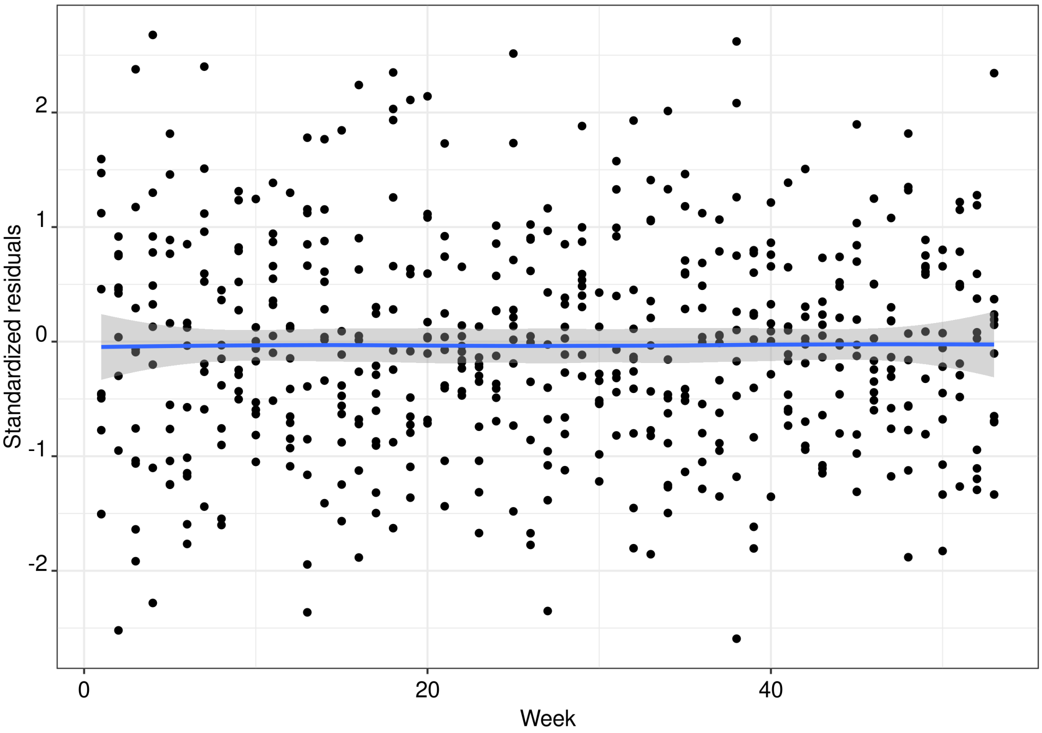

Figure B3: Red fox: residuals versus the weekly term of the AR1 model.

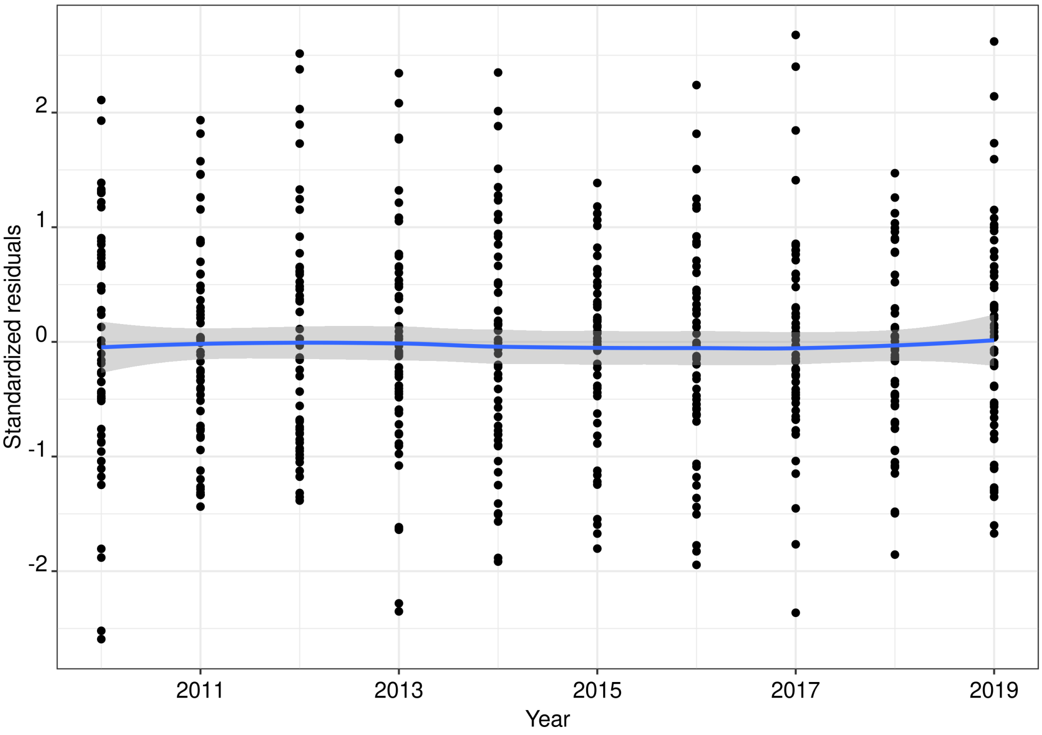

Figure B4: Red fox: residuals versus the yearly term of the AR1 model.

Wild boar (*Sus scrofa*)

Model	**WAIC**	**DIC**	**CPO**
No AR structure	1880.0	1878.9	-940.1
AR1*	1847.7	1844.8	-924.9
AR2	1834.3	1829.7	-7923.2
AR3	1833.9	1834.6	-2819.8

Table C - Comparison between the starting model and models with a 1st, 2nd and 3rd order autoregressive structure, accounting for temporal correlation. Indexes: Widely Applicable Information Criterion (WAIC), Deviance Information Criterion (DIC) and sum of log-converted Conditional Predictive Ordinal values (CPO). The best candidate model is highlighted.

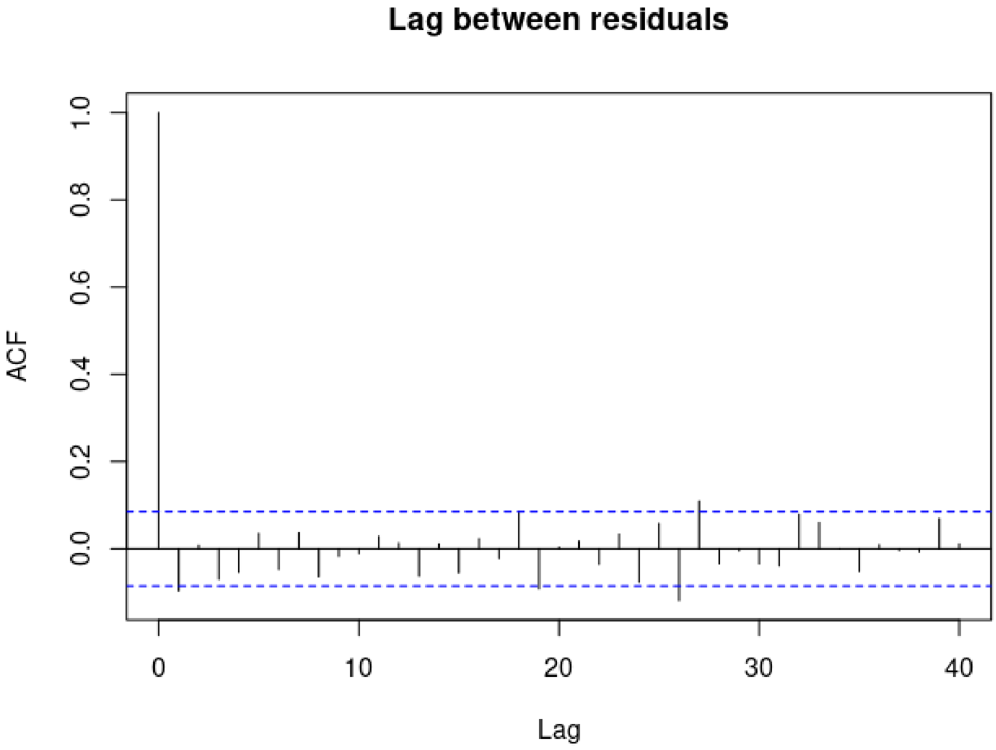

Figure C1: Wild boar: temporal lag between model residuals of the AR1 model.

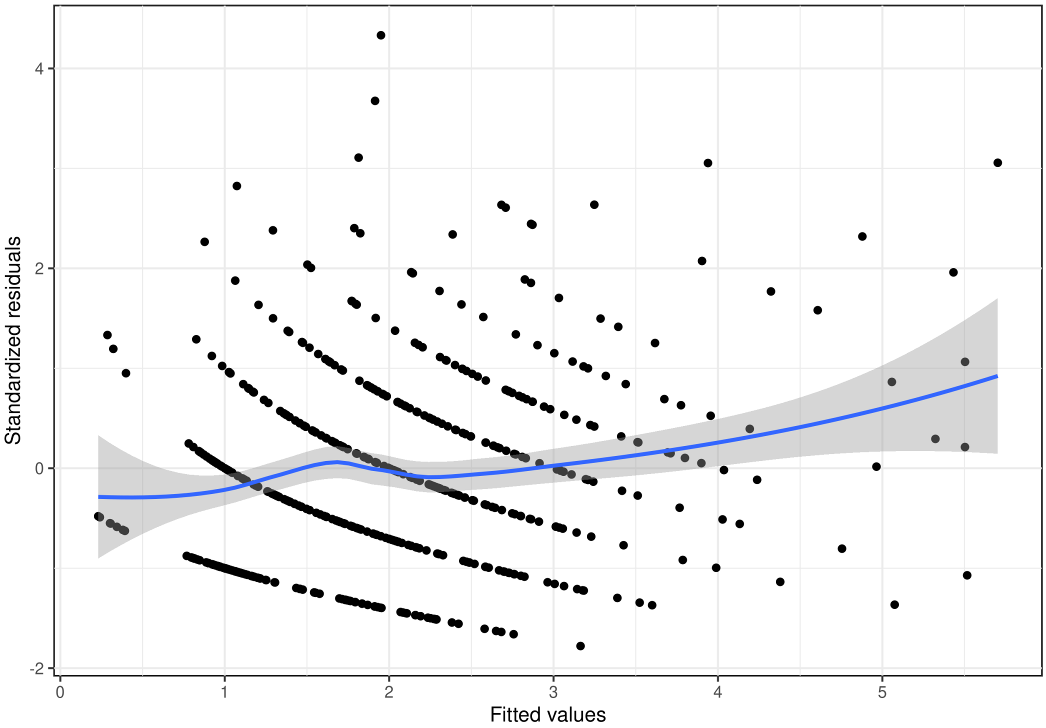

Figure C2: Wild boar: residuals versus fitted values of the AR1 model.

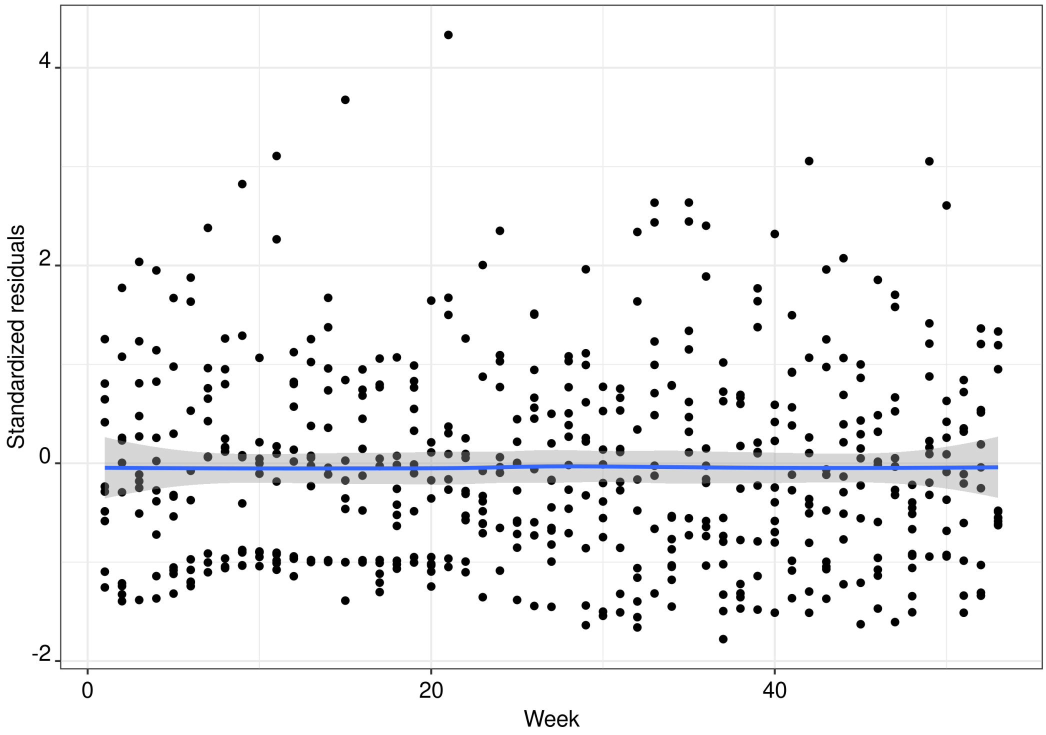

Figure C3: Wild boar: residuals versus the weekly term of the AR1 model.

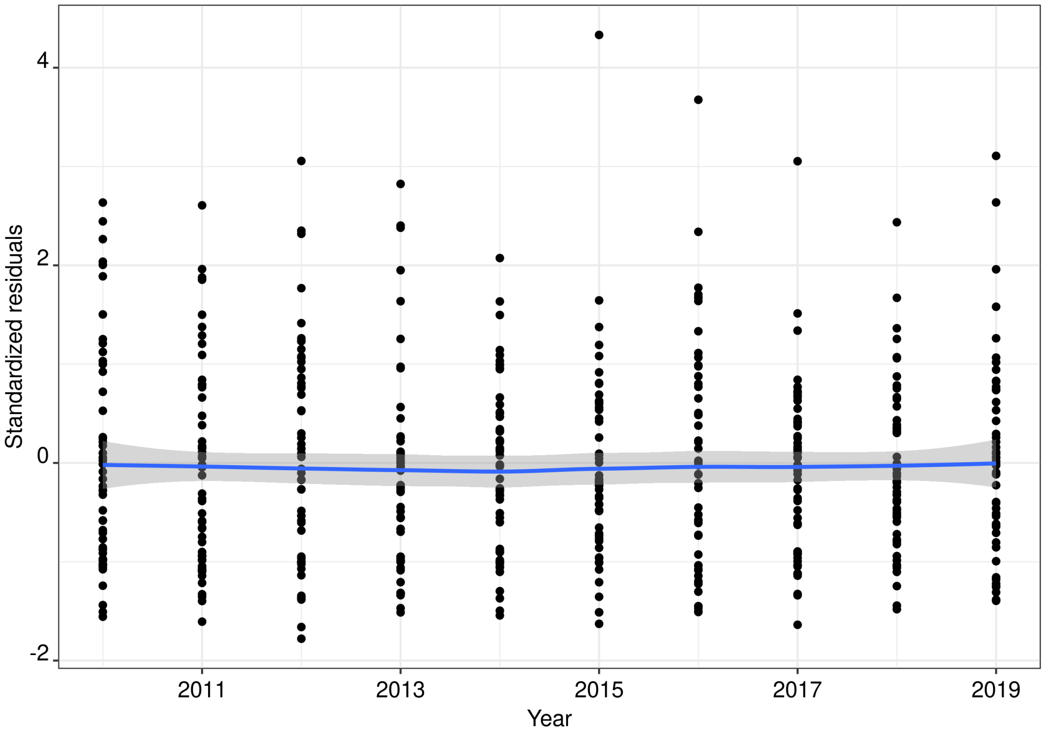

Figure C4: Wild boar: residuals versus the yearly term of the AR1 model.

European badger (*Meles meles*)

Model	WAIC	DIC	CPO
No AR structure*	2646.1	2640.5	-1323.3
AR1	2641.0	2636.4	-1321.2
AR2	2631.0	2624.7	-1317.8
AR3	2635.8	2632.1	-1319.6

Table D - Comparison between the starting model and models with a 1st, 2nd and 3rd order autoregressive structure, accounting for temporal correlation. Indexes: Widely Applicable Information Criterion (WAIC), Deviance Information Criterion (DIC) and sum of log-converted Conditional Predictive Ordinal values (CPO). The best candidate model is highlighted

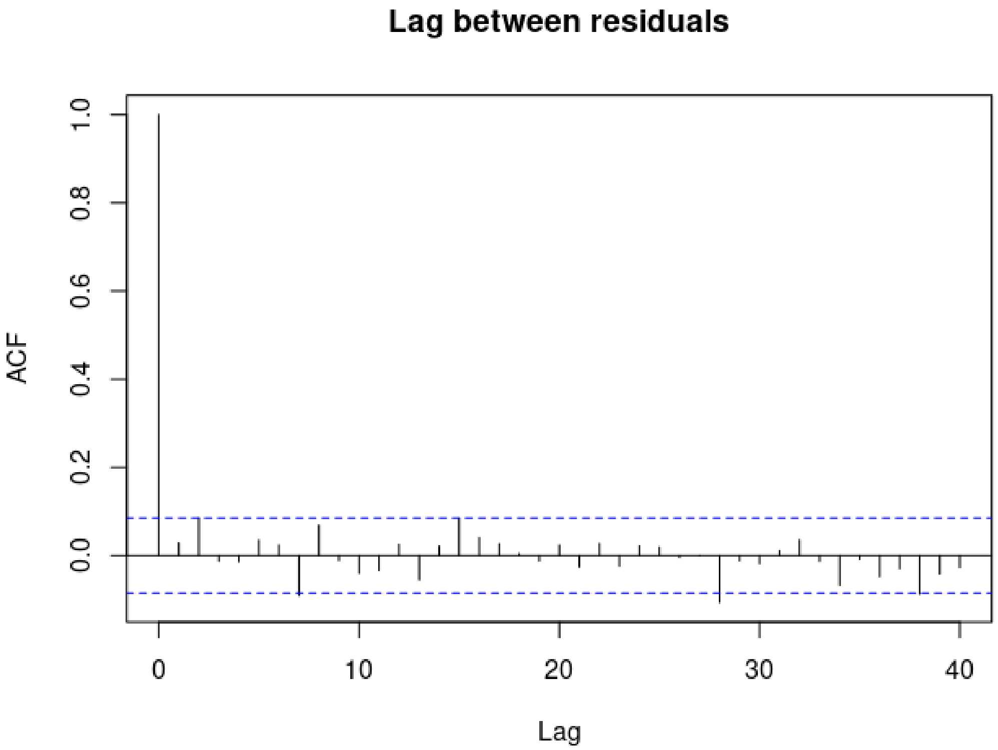

Figure D1: European badger: temporal lag between model residuals of the non-AR model.

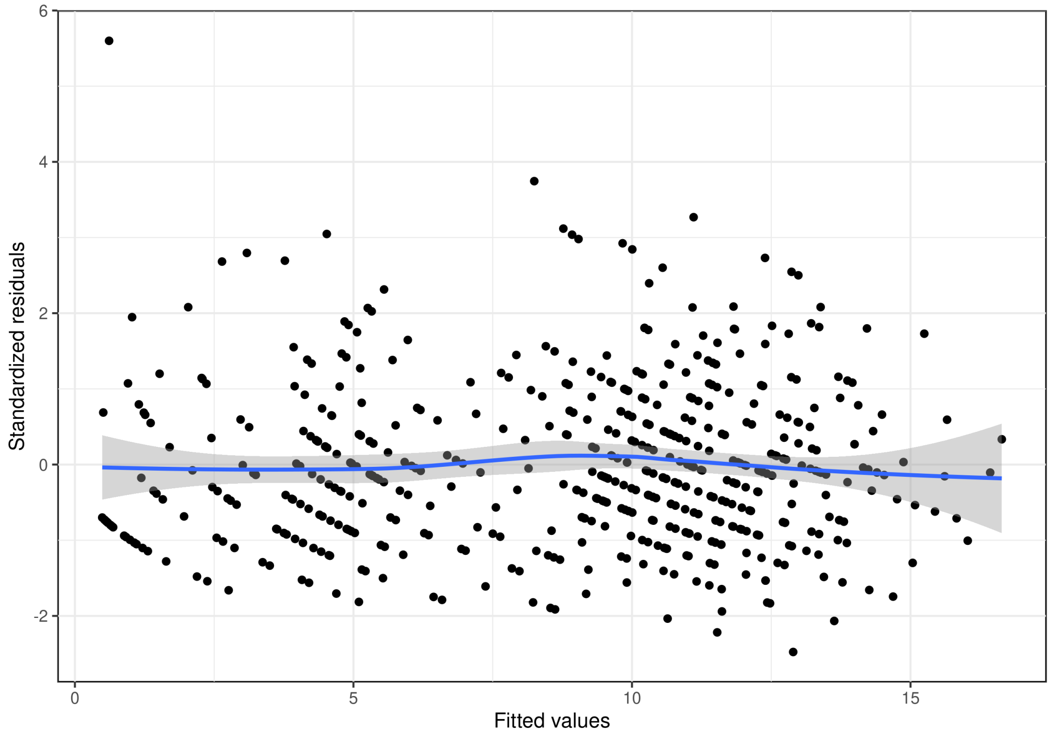

Figure D2: European badger: residuals versus fitted values of the non-AR model.

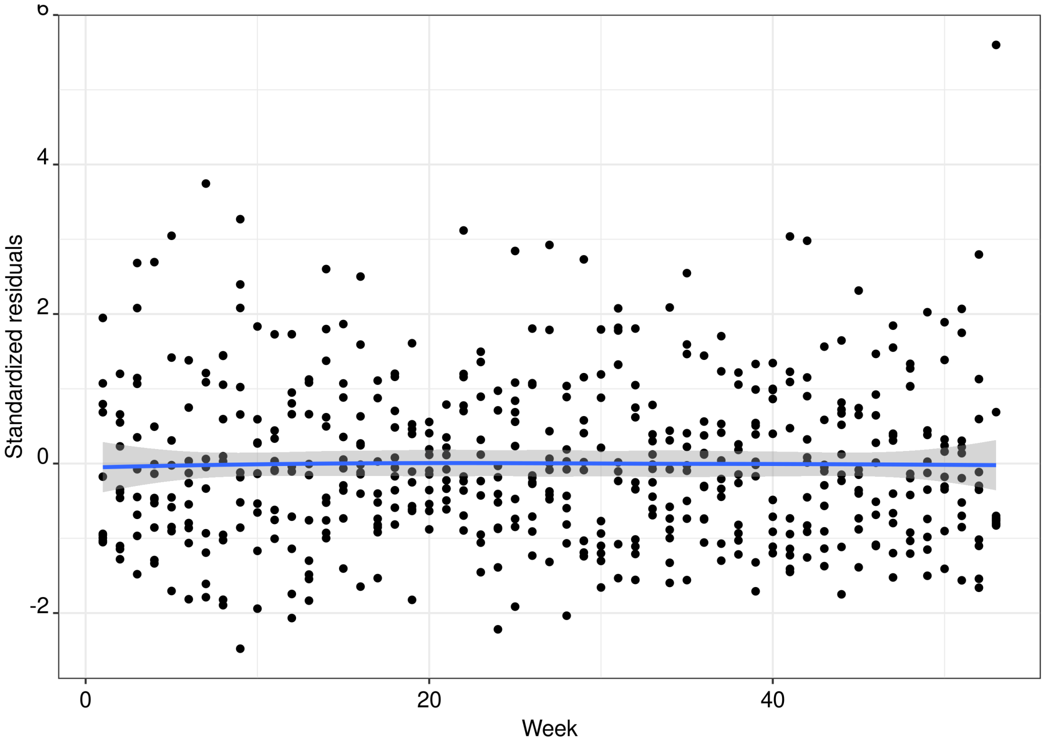

Figure D3: European badger: residuals versus the weekly term of the non-AR model.

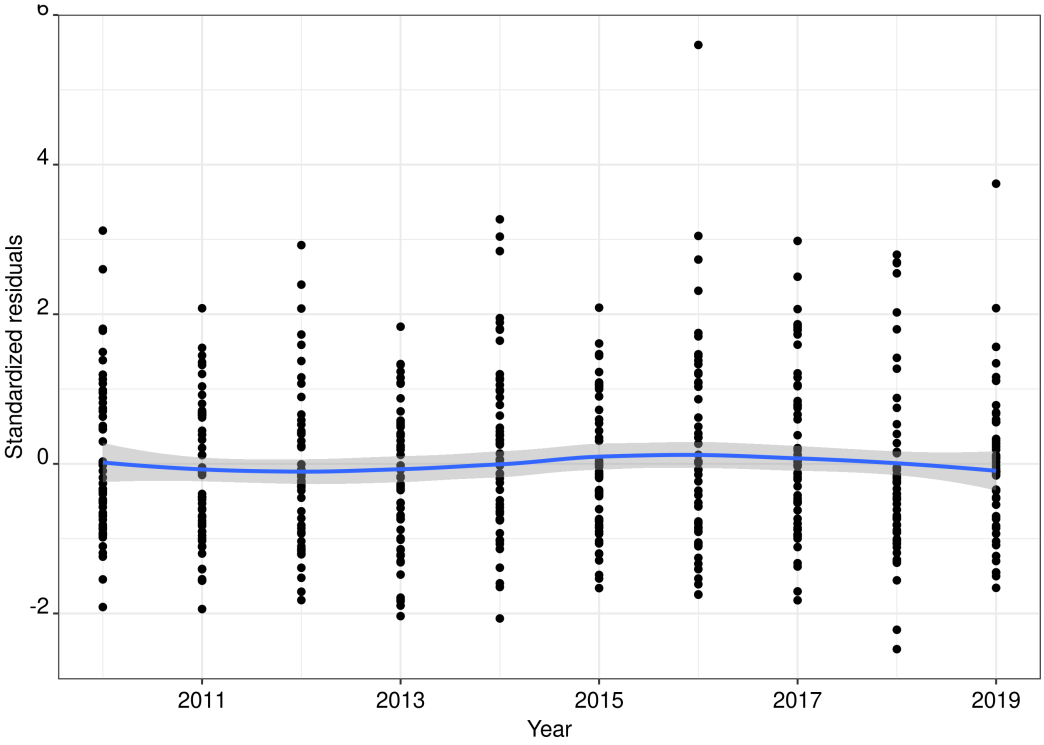

Figure D4: European badger: residuals versus the yearly term of the non-AR model.

Red deer (*Cervus elaphus*)

Model	**WAIC**	**DIC**	**CPO**
No AR structure	1757.9	1740.9	-889.4
AR1*	1722.6	1723.5	-861.3
AR2	1722.8	1723.9	-861.8
AR3	1723.0	1724.3	-862.6

Table E - Comparison between the starting model and models with a 1st, 2nd and 3rd order autoregressive structure, accounting for temporal correlation. Indexes: Widely Applicable Information Criterion (WAIC), Deviance Information Criterion (DIC) and sum of log-converted Conditional Predictive Ordinal values (CPO). The best candidate model is highlighted.

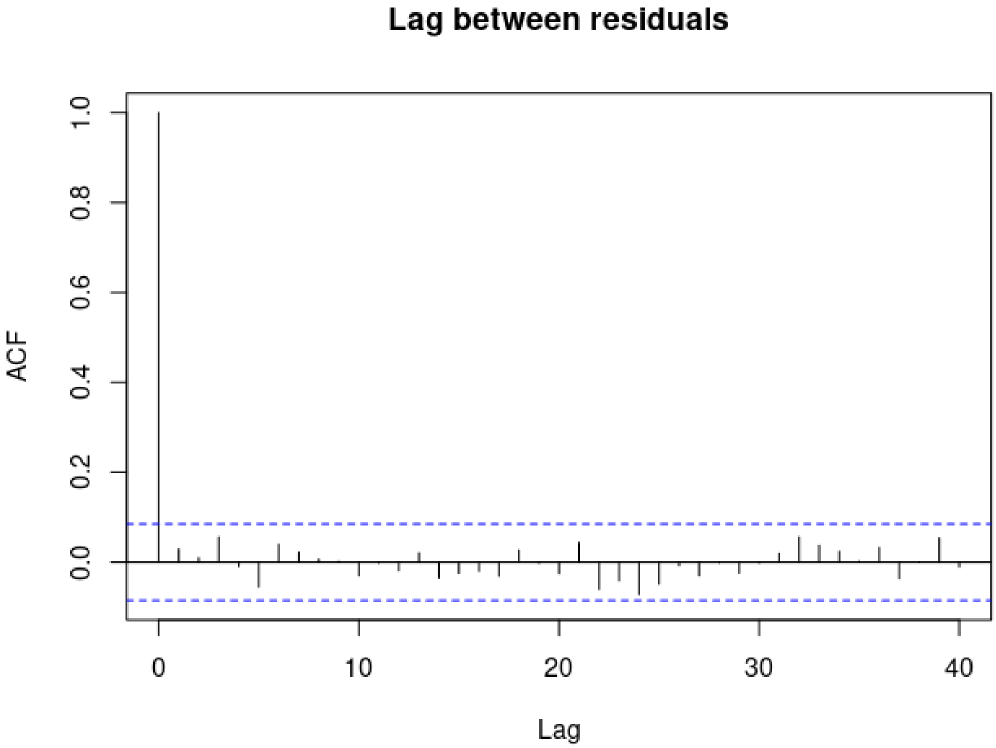

Figure E1: Red deer: temporal lag between model residuals of the AR1 model.

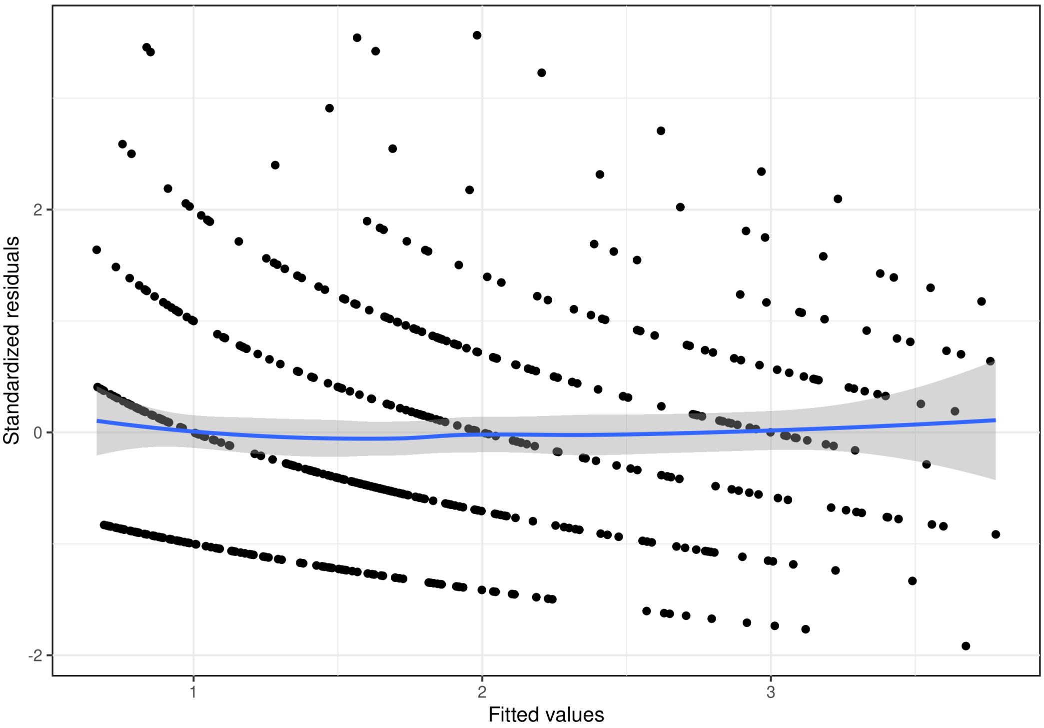

Figure E2: Red deer: residuals versus fitted values of the AR1 model.

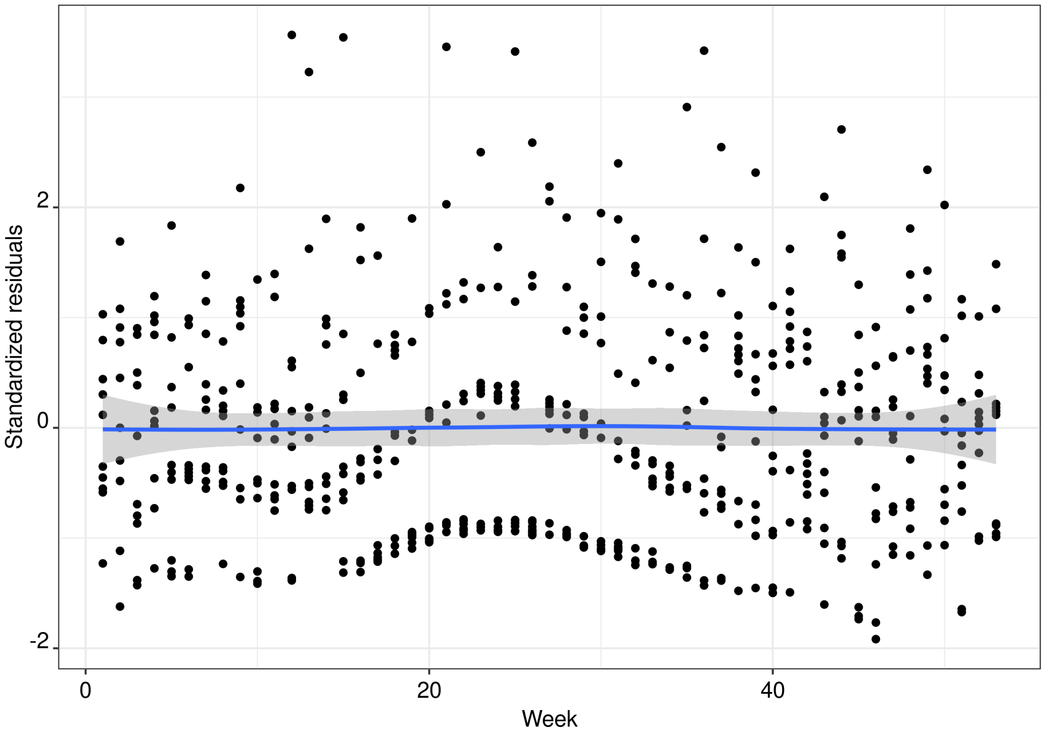

Figure E3: Red deer: residuals versus the weekly term of the AR1 model.

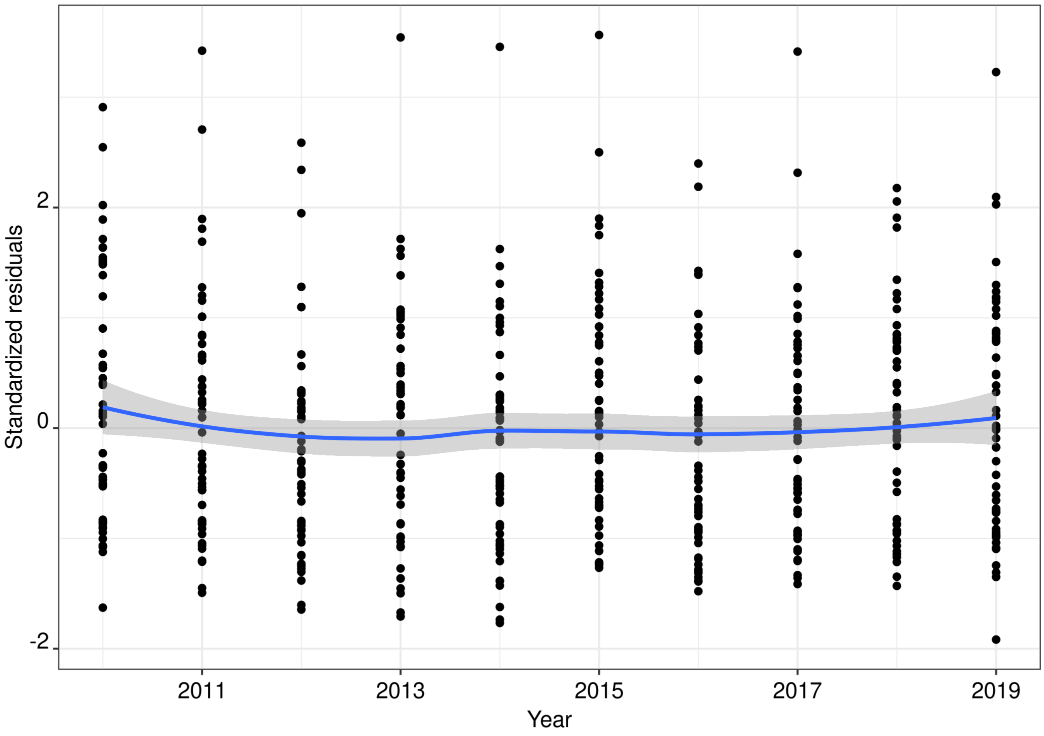

Figure E4: Red deer: residuals versus the yearly term of the AR1 model.

European brown hare (*Lepus europaeus*)

Model	WAIC	DIC	CPO
No AR structure	2721.1	2764.0	-1384.2
AR1[*]	2721.7	2716.9	-1362.7
AR2	2715.7	2710.8	-1362.2
AR3	2714.01	2709.5	-1361.5

Table F - Comparison between the starting model and models with a 1st, 2nd and 3rd order autoregressive structure, accounting for temporal correlation. Indexes: Widely Applicable Information Criterion (WAIC), Deviance Information Criterion (DIC) and sum of log-converted Conditional Predictive Ordinal values (CPO). The best candidate model is highlighted

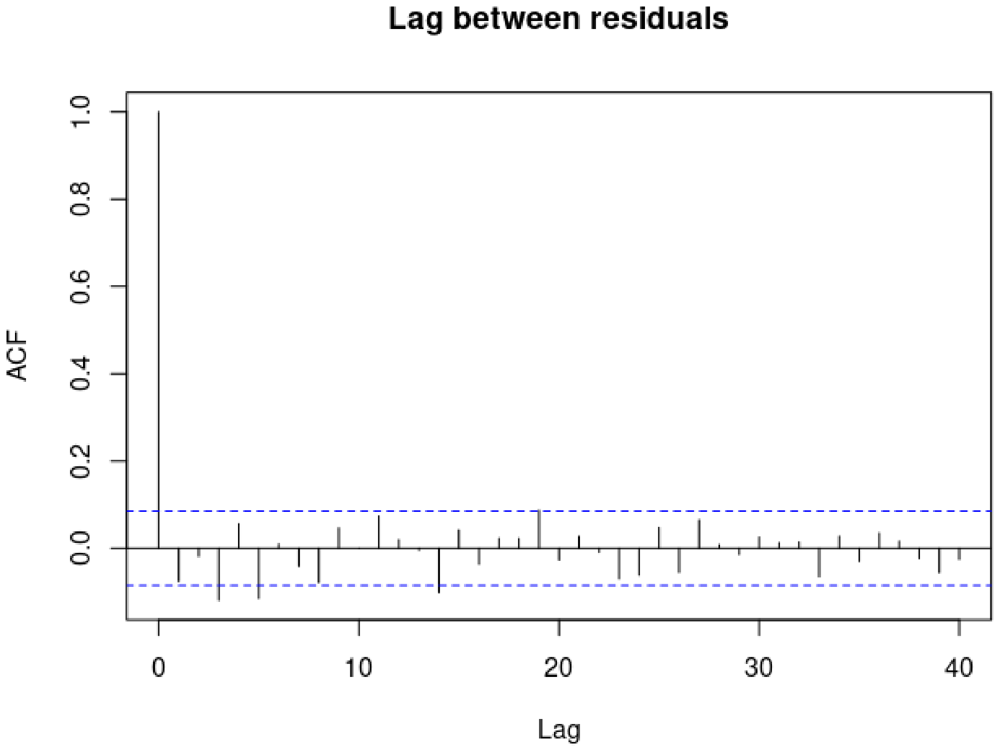

Figure F1: European brown hare: temporal lag between model residuals of the AR1 model.

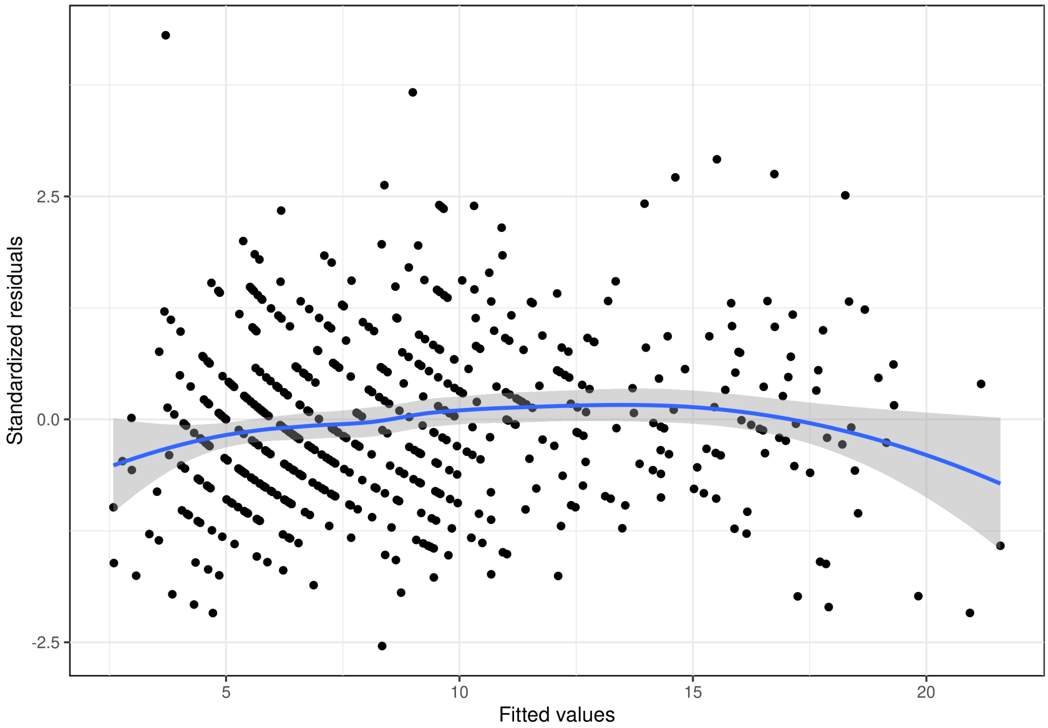

Figure F2: European brown hare: residuals versus fitted values of the AR1 model.

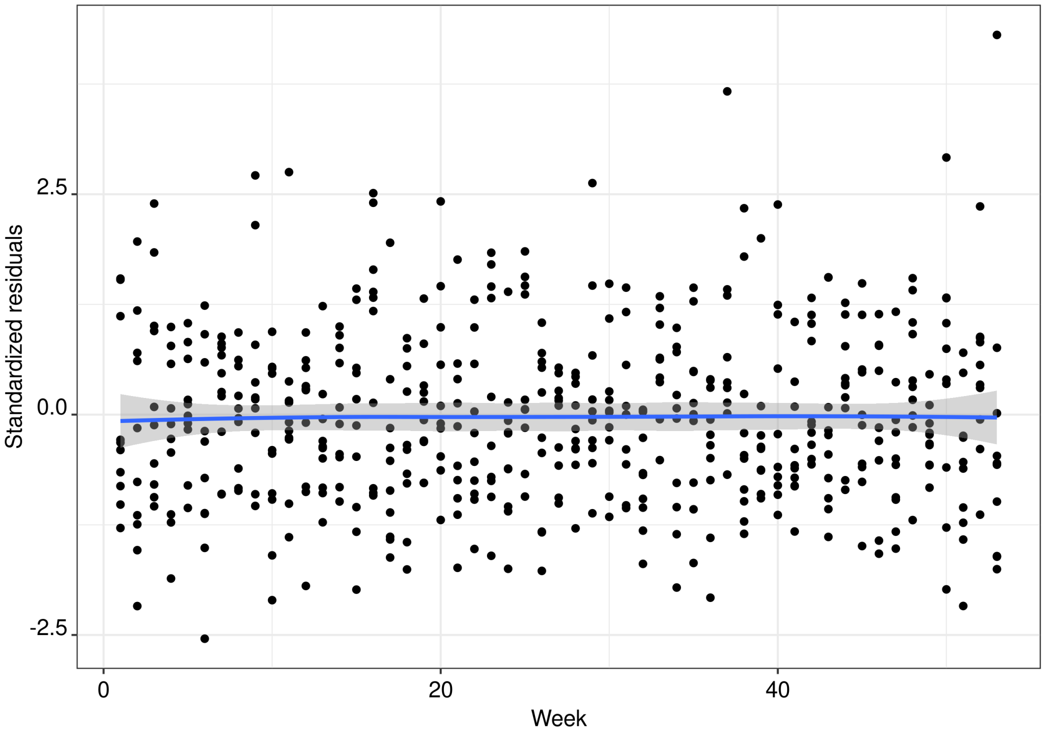

Figure F3: European brown hare: residuals versus the weekly term of the AR1 model.

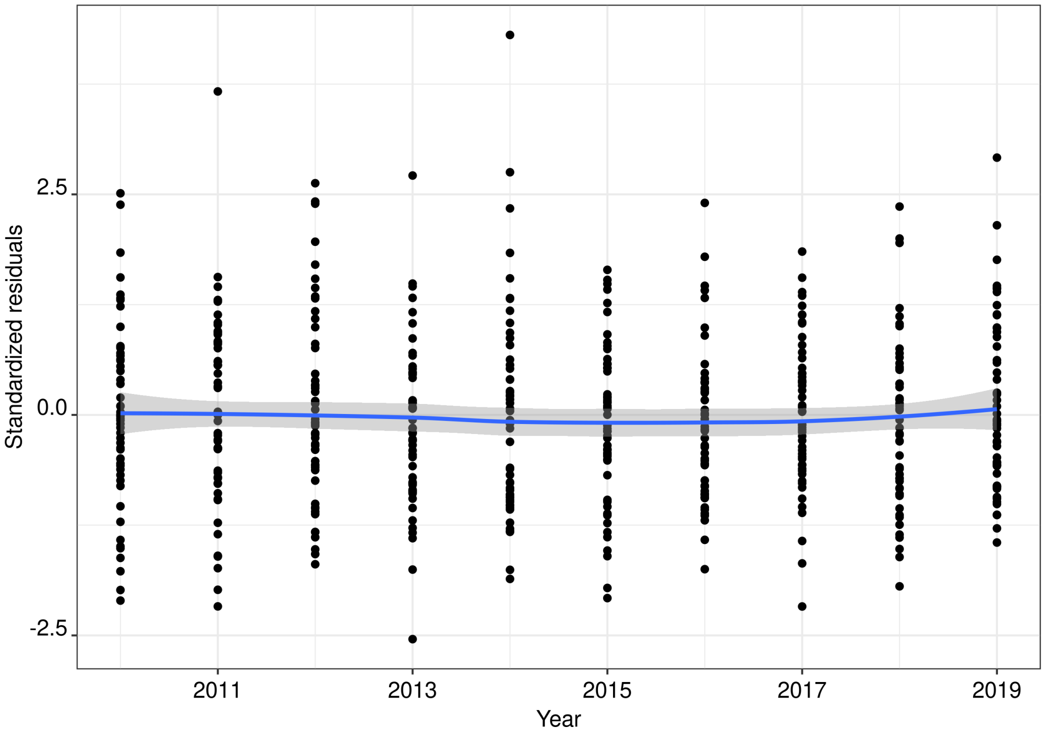

Figure F4: European brown hare: residuals versus the yearly term of the AR1 model.

Stone marten (*Martes foina*)

Model	**WAIC**	**DIC**	**CPO**
No AR structure	2587.7	2585.7	-1293.9
AR1*	2567.1	2567.4	-1283.8
AR2	2566.1	2566.9	-1283.4
AR3	2566.3	2566.8	-1283.6

Table G - Comparison between the starting model and models with a 1st, 2nd and 3rd order autoregressive structure, accounting for temporal correlation. Indexes: Widely Applicable Information Criterion (WAIC), Deviance Information Criterion (DIC) and sum of log-converted Conditional Predictive Ordinal values (CPO). The best candidate model is highlighted

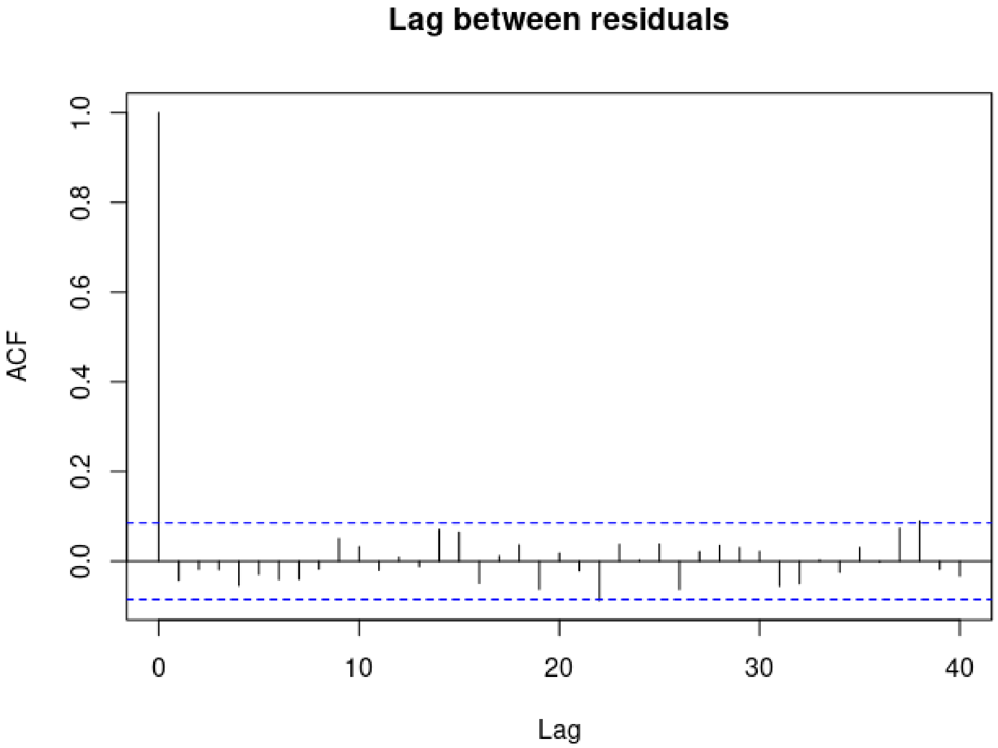

Figure G1: Stone marten: temporal lag between model residuals of the AR1 model.

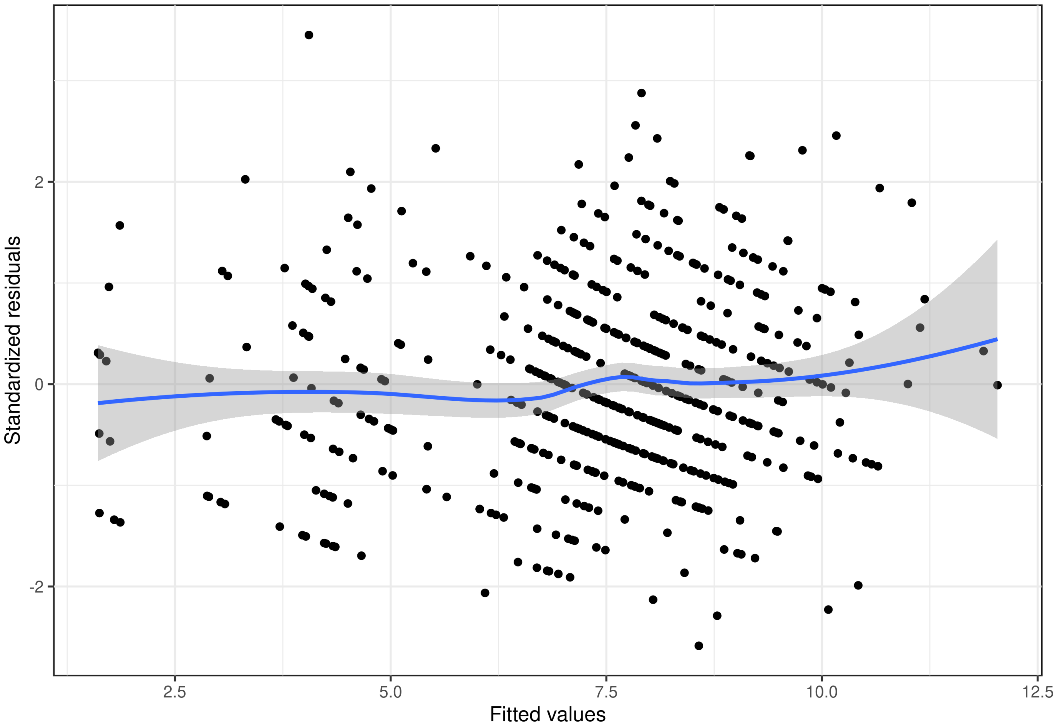

Figure G2: Stone marten: residuals versus fitted values of the AR1 model.

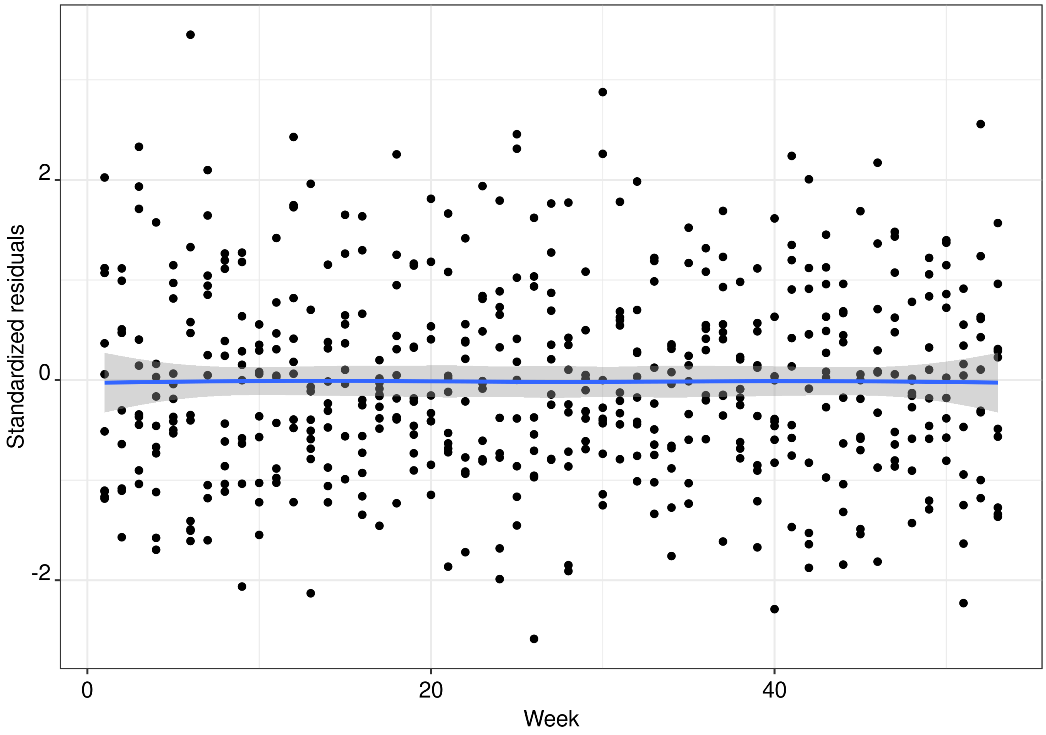

Figure G3: Stone marten: residuals versus the weekly term of the AR1 model.

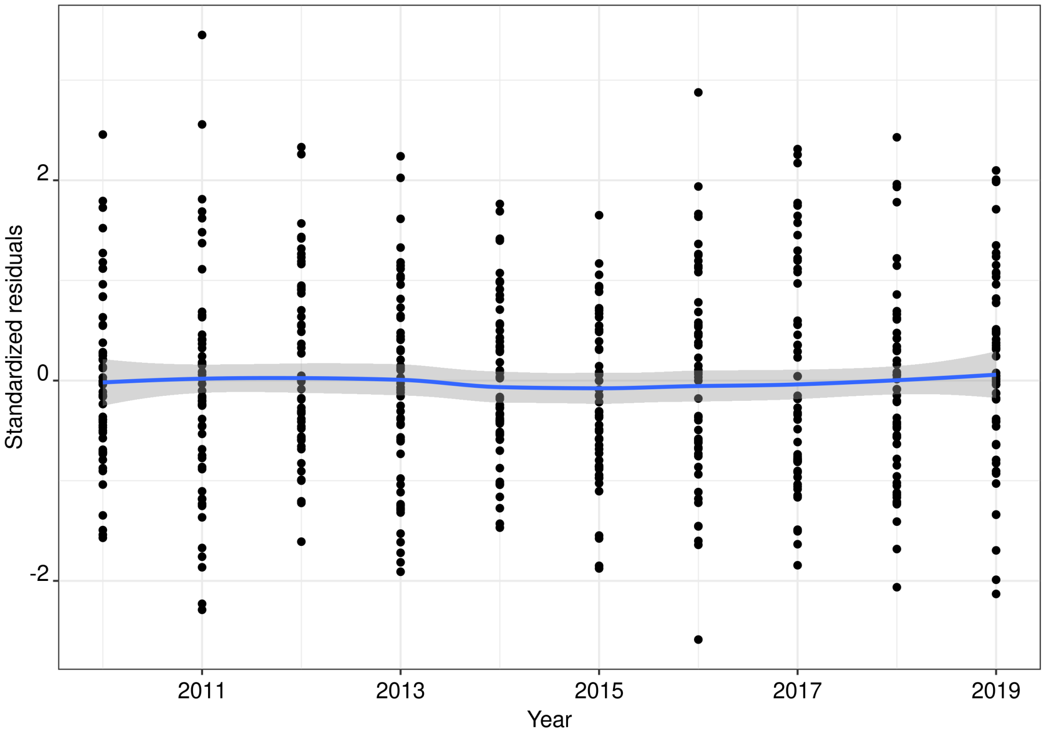

Figure G4: Stone marten: residuals versus the yearly term of the AR1 model.