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Predation on livestock as an indicator of drastic prey decline? The indirect effects of an African swine fever epidemic on predator–prey relations in Poland

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ABSTRACT

The gray wolf (*Canis lupus*) is one of the most conflictual mammals in Europe. Wild boar (*Sus scrofa*) are an essential part of gray wolf diet in central Europe, but after the emergence of African swine fever (ASF) in Europe, a sharp decline of the wild boar occurred. We examined how the wild boar population decline, due to African swine fever outbreak and mitigation efforts, affected the number of livestock killed by wolves in Poland using long-term data on wild ungulate and livestock population sizes and wolf-induced mortality between 2013 and 2019. We examined the influence of multiple factors on livestock kill rate, and the influence of wild boar population declines on the number of Cervidae killed by wolves using linear mixed models. We also explored the possibility of predicting a dramatic decrease in the wild boar population based on livestock depredation patterns. The number of livestock killed by wolves decreased with wild boar and roe deer (*Capreolus capreolus*) population size, and increased with red deer (*Cervus elaphus*) population size. A decline in the wild boar population was significantly correlated with an increase in the number of both red and roe deer killed by wolves. A drastic decline of wild boar population (over 30%) could be predicted by the numbers of livestock killed by wolves. Our study confirms that large changes in the number of naturl prey can increase livestock depredation, although these changes may be difficult to detect when the fluctuations in the numbers of natural prey are smaller. In our opinion, this indicates that the assessment of factors influencing livestock depredation should consider historical changes in prey dynamics. We suggest managers and conservationists use the predator population as a 'first alert system' for indirect monitoring of prey species. In this system, a sudden increase in wolf attacks on livestock across a large area of should trigger an alarm and prompt verification of the number of natural prey in the environment.

1. Introduction

Apex predators are an important component of ecosystem function. They shape the population size, behavior, spatial distribution, and physiological condition of prey (Okarma, 1995; Ripple and Beschta, 2012; Wikenros et al., 2015; Mattisson et al., 2016; Klich et al., 2020), and directly affect ecosystems by exerting top-down control on lower trophic levels (Ripple and Beschta, 2012). At the same time, predator populations are often challenging to manage, as they commonly come into conflict with humans, including depredating economically and culturally important livestock (Woodroffe et al., 2005; Aryal et al., 2014; McManus et al., 2015).

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The gray wolf (*Canis lupus*) is an important apex predator that affects both their prey populations as well as ecosystem function (Ripple and Beschta, 2012). After a period of long-term population decline in central Europe, wolf populations have increased, and their range expanded, over the last 20 years (Chapron et al., 2014). They are currently a common predator in much of Europe (Herzog, 2018). The wolf is also one of the most conflictual mammals in Europe, mainly due to frequent attacks on livestock (Graham et al., 2005; Fernández-Gil et al., 2016; Bautista et al., 2019), and the mechanisms and interventions to reduce this phenomenon are widely studied (Eklund et al., 2017; Gervasi et al., 2020; Janeiro-Otero et al., 2020). In general, ungulates are the main prey for wolves, although many other species and taxa can contribute to their diet (Okarma, 1995; Sidorovich et al., 2017). Prey composition and diet largely depend on the species available in the environment and, as a consequence of variation in prey vulnerability and density, wolf diet can vary significantly between regions. For example, wolves mainly hunt elk (*Alces alces*) and red deer (*Cervus elaphus*) in Scandinavia and in the Greater Yellowstone Ecosystem, respectively (Mech and Boitani, 2003; Hilde and Hjeljord, 2003; Lafferty et al., 2014; Latham et al., 2013). In central Europe, however, red deer, roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), and beaver (*Castor fiber*) are their main prey (Meriggi and Lovari, 1996; Žunna et al., 2009; Sidorovich et al., 2017), with livestock being a core component of diet in certain regions, such as in Greece (Migli et al., 2005). When wolves preferentially prey on one species, a decrease in that prey species density can cause significant changes in the composition of their diet (Murdoch and Oaten, 1975). Such a relationship was found for wild boar, when a decline in wild boar population size resulted in wolves switching to other ungulates in the deer family in Italy (Gazzola et al., 2007; Mori et al., 2017) and Belarus (Klich et al., 2021), or other food sources in Estonia (Valdmann and Saarma, 2020). However, wolves will not always shift to other prey species, for example, when dangerous species, such as American bison (*Bison bison*) that are large and aggressive, are the only other alternative (Mukherjee and Heithaus, 2013; Tallian et al., 2017). Wild boar are an essential part of wolf diet in central Europe. Depending on local conditions, wild boar may be the second or third order prey, and its contribution to consumed biomass may exceed 20% (Jędrzejewski et al., 2000; Nowak et al., 2011; Sidorovich et al., 2017). Research from Italy even indicates that wild boar may be the most important alternative wolf prey when the number of other ungulates declines (Mori et al., 2017).

In Poland, wolves currently inhabit all larger forest complexes (Nowak and Mysłajek, 2016), but this species is characterized by high plasticity in relation to occupied environments and diet preference. Current wolf diet is poorly understood in Poland, but recent studies show that wild boar are probably a second order prey, after red and roe deer (Wierzbowska et al., 2016). Moreover, the availability of prey largely shapes wolf diet composition (Okarma, 1995; Sidorovich et al., 2017), and a significant increase in the number of wild boar has been observed during last 20 years (Popczyk, 2016). The situation changed after the emergence of African swine fever (ASF) in Europe, which started in 2007 in Georgia and Russia, reaching Ukraine in 2012 and Belarus in 2013 (Cwynar et al., 2019). The virus first appeared in Poland in 2014, quickly spread across the country, and the number of infected wild boars grew rapidly (Woźniakowski et al., 2016; Pejsak et al., 2018).

African swine fever is a viral disease of *Suidae* with high transmission potential during direct contact with infected individuals or indirect contact with infected materials or objects (Penrith and Vosloo, 2009). Due to high mortality rates of infected domestic pigs, the disease poses an economic threat (Dixon et al., 2019). In an attempt to mitigate disease spread, wild boar hunting bags were dramatically increased, which resulted in a sharp decline of wild boar population across Poland (European Food Safety Authority, 2014). Thus, a situation arose in Poland where the wolves main prey populations suddenly declined (Morelle et al., 2020). On one hand, it can be expected that the wolf, an opportunistic predator, would switch prey and hunt other wild prey species more often (Okarma, 1995). On the other hand, wolves may make up for declines in wild prey abundance by increasing depredation of easy to kill livestock (Janeiro-Otero et al., 2020). However, in another study in Europe, variation in the abundance of a natural prey did not affect the impact of wolves on the sheep industry (Gervasi et al., 2020). Gervasi et al. (2020) suggested that the historical context of wolf presence in a given area might explain the persistence of livestock predation. A significant decrease of wild boar population as a result of African swine fever in Estonia mainly caused an increase in the use of other prey and plant material by wolves (Valdmann and Saarma, 2020). Mori et al. (2017) speculated that the heavy artificial reduction of wild boar numbers would deprive the wolf of a primary prey species, thus intensifying predation on roe deer and livestock. A decline in wild boar due to African swine fever in Belarus resulted in higher predation on roe deer and red deer, but not livestock (Klich et al., 2021). Here, the authors suggested that the lack of livestock depredation was because wolves were heavily hunted in the region.

We examined how wild boar population reduction, due to the African swine fever epidemic and its mitigation efforts, affected the number of livestock killed by wolves in Poland between 2014 and 2019. We focused on the following research hypotheses: 1) livestock depredation increased as a result of wild boar population decline and 2) prey population declines can be predicted via livestock depredation monitoring. The second hypothesis is based on the assumption that minor changes in the number of natural prey will not significantly affect livestock depredation. However, a steep decline in prey population size will be detectable in livestock depredation monitoring data. This would suggest that the natural influence of prey is usually difficult to detect, because the fluctuation in their numbers is not large.

2. Methods

2.1. Study area

The study was conducted in Poland, which covers 312,696 km^2 and has an estimated 38.4 million people. Poland is divided into 16 main administrative units called 'voivodeships' (the highest-level of administrative division) (statistical office https://stat.gov.pl). Poland contains 4,696 hunting grounds encompassing 252,546 km^2.

2.2. Data collection

In order to achieve the aim of the research, we obtained data on: a) population numbers of ungulate game animals (roe deer, red deer, wild boar, and elk) and wolves, b) the number of livestock (horses, cattle, goats, sheep, and farmed (fallow and red) deer), c) the number of wild ungulates killed by wolves, d) number of livestock killed by wolves, and e) the number of ungulate game animals (roe deer, red deer, and wild boar) killed by hunters. The analyses included data collected between 2013 and 2019 (except for wild boar, where data of population numbers covered years 2012–2019), which spanned the period before and after the African swine fever outbreak in Poland. All data, regardless the source, were collected at the voivodeship level, because we were not able to gather more detailed data for livestock depredation.

2.2.1. Wild animal population size and kill numbers

Data on population numbers of game animals, numbers of game animals killed by wolves, and hunted by hunters were collected from Polish Hunting Association. Hunting in Poland is limited to members of the Polish Hunting Association, in hunting grounds rented by hunting clubs. Each hunting club is obliged to prepare an annual hunting report which includes, among other information, estimated game population sizes, total annual harvest per species, other causes of mortality of all game species including predation by domestic dogs (*Canis familiaris*), wolves, lynx (*Lynx lynx*) and brown bears (*Ursus arctos*). The annual inventory and estimates of game species populations are used to plan harvest quotas for the following hunting season. The population census of all game species is estimated annually by hunters, who are obliged to implement several methods such as distance sampling, drive counts, snow tracking, plot sampling, and direct observation. Data on number of wolves were obtained from the Central Statistical Office (statistical office https://stat.gov.pl).

2.2.2. Livestock numbers and depredation

Data on the total number of livestock in each voivodeship were obtained from the Central Statistical Office (https://stat.gov.pl). Data on number of livestock killed by wolves in each area were collected from Regional Directories of Environmental Protection (RDEP). In Poland, depredation of livestock by wolves, lynx, and brown bears is compensated by the Polish government. Each case reported by a farmer is verified by designated employees of the RDEP, in consultation with veterinarians and hunting club representatives. Annual reports including information of depredated livestock are prepared by the RDEP. Regarding livestock, we included the following animal species in our analyses: horses, cattle, goats, sheep, and farmed (fallow *Dama dama* and red) deer. Other animals were excluded: dogs (they are not killed for food but as a result of competition), rabbits, and poultry (they can also be a prey for feral dogs and mesopredators). Livestock does not include pigs, as they are not at risk from wolf depredation due to their closed type of farming.

2.3. Data Analysis

2.3.1. Temporal trends

We examined the temporal trends in the total number of wild ungulates in Poland and the number of livestock killed by wolves using population estimate data and the number of reported livestock depredations in Poland. We also explored how the number of wild boar and livestock killed by wolves shifted across voivodeships in Poland between 2013 and 2019. To examine changes in the abundance of different prey (wild and livestock) killed by wolves during our study period, we generated a heat map that showed the overall the abundance of animals killed by wolves over the study period. Here, the number of ungulate species killed by wolves was normalized to 1 followed by transforming to $\log_{10}$ (colour intensity ranging from black: $\leq$0.01% to yellow: $\geq$10%), and presented using heat maps for visual inspection. To explore variation in the number of wild prey (wild boar, roe deer, and red deer) killed by wolves and hunters during our study period, we generated and compared boxplots for each year (y-axis) of wild prey killed by wolves and hunters (x-axis $\log_{10}$ transformed). The heat map and boxplots were generated in the R environment (R Core Team, 2020) using tidyverse package (Wickham et al., 2019).

We also displayed changes in livestock depredation patterns and wild boar numbers over time on the map of Poland. We added the following data to the maps: 1) the number of wild boar in 2013 and 2019, per 100 km^2, 2) the number of wild boar killed by wolves in 2013 and 2019, and 3) the number of livestock (horses, cattle, sheep, goats) killed by wolves in 2013 and in 2019, per 100 km^2, 4) the range of wolves in 2013 (the layer of the map was prepared on the basis of data published by Mammal Research Institute of Polish Academy of Sciences: https://ibs.bialowieza.pl/) and 2019 (the layer of map was prepared on the basis of Mammals' Atlas of Polish Academy of Sciences: https://www.iop.krakow.pl/). For the thematic maps 1, 2, and 3 we excluded four voivodeships where the wolf population was not present or at very low numbers which resulted in the lack of livestock depredation (Lubelskie, Łódzkie, Opolskie and Świętokrzyskie voivodeships). For two other voivodeships (Mazowieckie and Kujawsko-Pomorskie), we presented data for 2018 instead 2019, because of a lack of data. The maps were generated in MapInfo Software version 11.0 in Transverse Mercator Projection with special Polish parameters (Coordinate System: EPSG 2180).

2.3.2. Wild boar, livestock depredation, and Cervidae kill rates

To assess the influence of different factors on the kill rate of livestock, we used a linear mixed model (LMM) in R (Lme4 package). LMMs account for correlation between multiple observations taken unique sampling units. We therefore included voivodeship a random factor to account for correlation between livestock mortalities. Models were estimated using adaptive Gaussian quadrature with parameters estimated from maximum likelihood. In all models, the number of livestock killed by wolves was a dependent variable. We used five explanatory variables: 1) roe deer population numbers (ROE), 2) red deer population numbers (RED), 3) wild boar population numbers (BOAR), 4) wolf population numbers (WOLF) and 5) livestock numbers (LIVESTOCK). We also included interactions of all variables with the wild boar population numbers (ROE*BOAR, RED*BOAR, WOLF*BOAR and LIVESTOCK*BOAR). Interactions were used to consider the wolf's different response to wild boar decline in areas where natural prey were fewer or more numerous, or the availability of livestock was limited. We did not include elk population numbers, as this species was not present, or it was present in very low numbers, in most voivodeships. Higher correlations among variables were found only in pairs: roe deer - red deer ($r = 0.767$, $p < 0.001$) and roe deer - wild boar ($r = 0.587$, $p < 0.001$). To meet model assumptions of normality, we log transformed the response variable. To avoid very high scale differences between independent variables, we performed a normalization of each variable. We did not include voivodeships where the wolf population was not present or at very low numbers (Lubelskie, Łódzkie, Opolskie and Świętokrzyskie voivodeships), as this resulted in the lack of potential livestock depredation in these regions. Model selection was based on Akaike information criterion adjusted for small sample size (AIC_c) (Burnham and Anderson, 2002). The best-fit models had the lowest AIC_c score, and we considered all models with a $\Delta AIC_c < 2$ plausible according to Burnham and Anderson (2002). We explored all possible combinations of the explanatory variables and compared them to a null, intercept only model. Final model parameters and 95% confidence intervals (95% CI) were estimated by model averaging all model with a $\Delta AIC_c < 2$ (modavg package). We assessed model fit with a normal Q-Q plot, histogram of residuals, and fitted vs residuals plot (Supplementary Fig. A1.)

We also ran a similar linear mixed model that also included a random slope for the wild boar population numbers (1 + WILD | VOIVODESHIP) according to Winter (2013) to assess the response of killed livestock on the wild boar population in each voivodeship. We similarly used the same set of variables and interactions. We also performed a similar model selection as above and analysed the best model (with the lowest AICc) with regard to coefficients.

To assess the influence of wild boar population decline on the number of Cervidae killed by wolves, we again used LMMs in R. We ran two similar models where the number of roe deer or red deer killed by wolves were the dependent variable, respectively. Wild boar population numbers were the explanatory variable in both models. To meet model assumptions, we log transformed the response variables. Similar to above, we included voivodeship as a random factor in both models, and, once again, we did not include voivodeships where the wolf population was not present or at very low numbers. We similarly performed a model selection as above.

2.3.3. Prediction of prey population drastic decline

In order to determine whether a decrease in the number of wild boar could be observed in livestock depredation rates, we compared two logistic regression models. We performed mixed logistic regressions in the Lme4 package. We based on the threshold for the definition of population drastic decline of 30% population numbers below the reference value. We used this threshold because the common threshold for a species to be considered vulnerable is a decline $\geq$ 30% of the population size (www.iucnredlist.org). According to this threshold, we determined the values of the dependent variable in the model. In Model A (decline) all cases (in a given year and in given voivodeship) for which the wild boar population size was more than 30% lower than the reference value, were marked as 1. Cases for which the population size was equal to or higher than the reference value were marked as 0. Other cases in which the number of the wild boar was lower up to 30% than the reference value, were omitted. In the second regression – Model B (fluctuation), values 0 were the same and all cases in which the number of the wild boar did not decrease more than 30% than the reference value were marked as 1. The values marked as 1 in the Model A were omitted (Fig. 1). The reference level was the population size of wild boar in 2012 (a year before the studied period, which presented comparable numbers of wild boar to the first years of study and before the population decline) for each voivodeship. This simple comparison allowed us to examine whether wild boar fluctuation ≥ 30% decrease would significantly relate to number of killed livestock (log transformed), which was an independent variable in the model. In all regression models, voivodeship was included as a random factor. Two similar models were built for a threshold of 20% to check whether the population drastic decline could be also defined as population decline over 20% from the reference value. We used 65 observations for the model of 30% threshold and 70 observations for the model of 20% threshold.

3. Results

3.1. Temporal trends

Wild boar numbers in Poland decreased from ~ 257,000 to ~ 66,000 individuals between 2013 (before ASF outbreak) and 2019 (after ASF outbreak) (Fig. 2). The largest decline occurred between 2017 and 2018, when the population fell from ~ 198,000 to ~ 82,000. Roe deer and red deer populations were generally stable through time, with a slight increase in numbers in 2017. The elk population consistently increased during the period of study, from ~ 12,000 to ~ 24,000 in 2019. Between 2013 and 2019, the number of livestock killed by wolves almost doubled, going from 1,148 to 2,135 individuals, with high variation in livestock depredation between years (Fig. 2). The wolf population also increased during this time period, from 932 to 2,745 individuals (Fig. 2).

The heat map of animals killed by wolves across years showed that the killing of animals, both wild and livestock, increased since 2015. This trend, however, was disrupted in 2018, when the number of animals killed by wolves, especially domestic animals, decreased (Fig. 3).

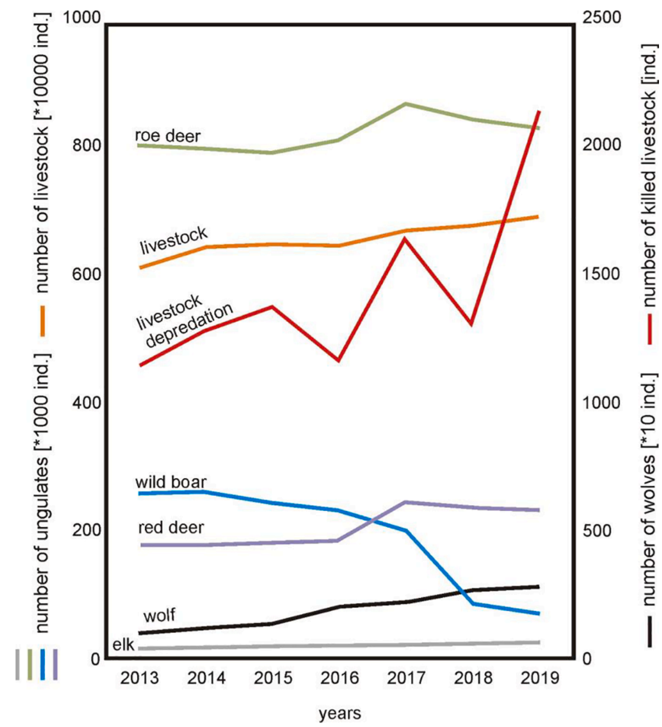

Fig. 2. Trends in the population size of wolves, primary wolf prey (roe deer, red deer, elk and wild boar) and livestock, as well as the number of livestock killed by wolves (i.e., livestock depredation of horses, cattle, goats, sheep, and farmed fallow and red deer) between 2013 and 2019 in Poland.

Wolf predation patterns on wild boar also shifted across Poland from 2013 to 2019. Wolves mainly preyed on wild boar in the north-eastern and southern parts of Poland in 2013, while in 2019, wild boar were heavily preyed upon in almost all western voivodeships, as well as in central and south-eastern Poland (Fig. 4). Livestock were mainly depredated in the northern and southern voivodeships in 2013. Comparatively, the number of livestock depredations was higher across the majority of Poland in 2019, except for several voivodeships in

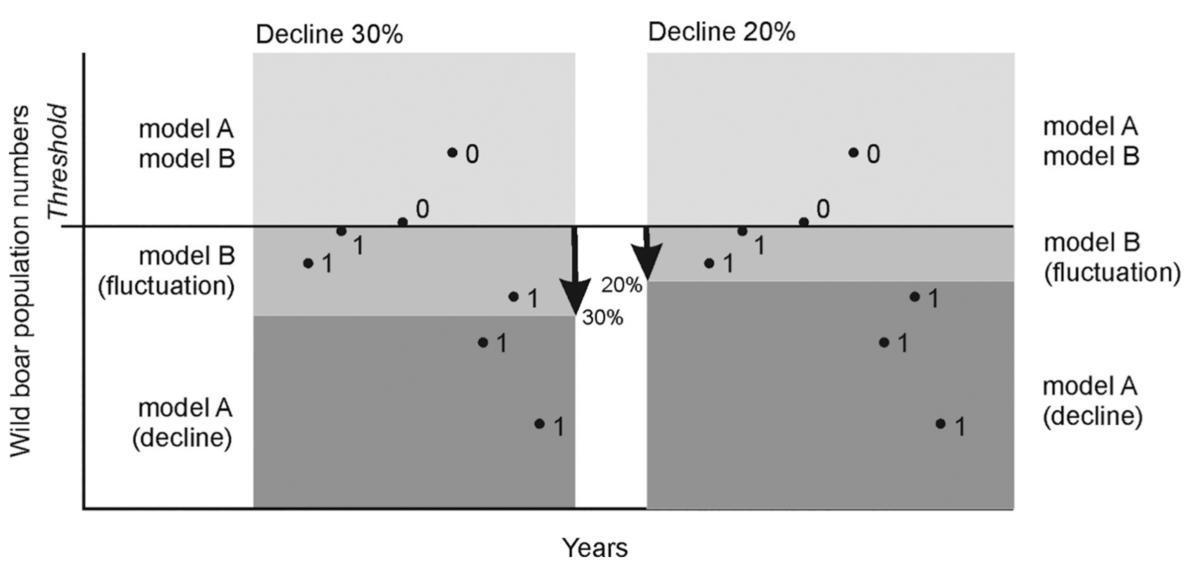

Fig. 1. Graphical description of value designation for dependent variable in mixed logistic regression models (A and B) based on the threshold (wild boar population number in 2012). Cases for which the population size was equal to or higher than the reference value - always marked as 0. Cases for which the wild boar population size was more than 30% (or 20%) lower than the reference value were marked as 1 in Model A (decline) and omitted in Model B (fluctuation). Cases for which the wild boar population size did not decrease more than 30% (or 20%) than the reference value were marked as 1 in Model B (fluctuation) and omitted in Model A (decline).

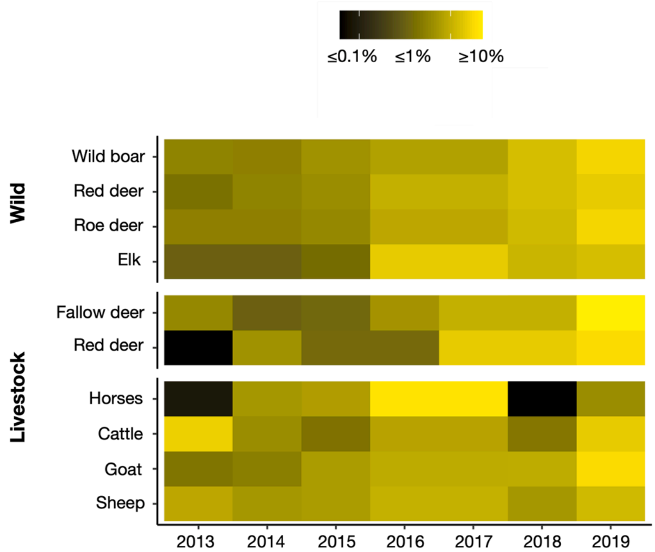

Fig. 3. Heat map showing the proportion of ungulates (categorised into wild and livestock) killed by wolves between 2013 and 2019 in percent change compared to the previous year. The colour intensity is presented in $\log_{10}$ and shows relative number of ungulates killed by wolves between consecutive years (black colour represents no killing of ungulates while brighter yellow represents higher number of killings between the years). The colour indicates percent change of killings between consecutive years (black: $\leq$0.01% of killing, yellow: $\geq$10% of killing).

central Poland (Fig. 4).

The number of wild boar killed by wolves was below average in 2013, remained steady between 2014 and 2017, and increased starting in 2018 (Fig. 5A). This closely corresponds to the predation patterns observed with roe deer and red deer across the same time period (Fig. 5B, C). While the number of roe and red deer harvested by hunters in Poland remained relatively steady through time (Fig. 5B, C), the number of wild boar harvested was below average in 2013, steady from 2014 through 2018, and declined in 2019 (Fig. 5A).

3.2. Wild Boar, livestock Depredation, and Cervidae kill rates

The final AIC_c model set for livestock depredation included two models with a $\Delta AIC_c < 2$ (Supplementary Table A1). The top model included wild boar, roe deer, and red deer population sizes, while the second-best model also included the total number of livestock (Supplementary Table A1). The number of livestock killed by wolves decreased with wild boar and roe deer population size and increased with red deer population size (Supplementary Table B1, Fig. 6). Livestock numbers appeared to be important in the number of livestock depredated in Poland (i.e., it was retained in 1 of 2 top models), however, the direction of the effect was inconclusive (i.e., the 95% CI for livestock overlapped 0) (Table B1, Fig. 6). We found no evidence for interactions between any of the prey population's sizes, i.e., no interaction terms were retained in the top models. We also found no evidence of a wolf effect, i.e., the term for wolf population size was not included in any of the top models.

The best random model (with random intercept and random slope for wild boar population numbers) included similar set of variables as in the above averaged models (BOAR, ROE, RED and LIVESTOCK). In all voivodeships, the predation rate of livestock responded similarly to wild boar population numbers (Table 1). In all viovodeships the coefficient for the wild boar was negative, but in two of them the reaction was weak (Małopolskie and Podkarpackie voivodeships), close to fixed ROE and RED (Podkarpackie) or even lower than coefficients of all fixed factors (Małopolskie).

A decline in the wild boar population was significantly correlated with an increase in the number of both red and roe deer killed by wolves. In both models, wild boar population numbers were negatively correlated with the number of deer killed by wolves. In the case of roe deer, the difference between the null model and the model with wild boar population was greater than in case of red deer (Table 2).

3.3. Prey population drastic decline

For the 30% threshold, a decrease of population size up to 30% couldn't be predicted by the number of livestock killed by wolves in model B (fluctuation) ($B_{\text{killed livestock}}$ = -0.027 ± SE 0.324, $p = 0.934$, $N = 57$). However, for this threshold, the probability of wild boar population drastic decline in model A (decline) (over 30% decrease in the population numbers comparing to the reference level) could be predicted by the numbers of livestock killed by wolves (Fig. 7). For the 20% threshold, both models were statistically insignificant. The wild boar drastic decline, defined as population numbers lower than a reference level, could not be predicted based on the livestock killed by wolves ($B_{\text{killed livestock}}$ = 1.0203 ± SE 0.5814, $p = 0.079$, $N = 70$). Similarly, a decrease of population size up to 20% below the reference value couldn't also be predicted by the number of livestock killed by wolves ($B_{\text{killed livestock}}$ = −0.183 ± SE 0.435, $p = 0.673$, $N = 53$).

4. Discussion

In accordance with our predictions, the number of wolf-livestock depredations in Poland was strongly correlated with the population sizes of their primary wild ungulate prey. This is consistent with observations that a decline in primary prey abundance alters wolf diet composition, including a shift from wild to domestic ungulates (Mori et al., 2017; Janeiro-Otero et al., 2020). Interestingly, the population size of wild boar, a secondary prey species for wolves in Poland, appeared to be a particularly strong driver of livestock depredation. However, wild boar populations underwent a dramatic decline during our study period due to nation-wide African swine fever mitigation efforts. In all voivodeships, livestock predation was tied with a decline in the wild boar population (Table 1.). Nevertheless, in two voivodeships in southern Poland (Małopolskie and Podkarpackie) this trend was much weaker. This is probably the result of a small number of wild boar populations in these areas as well as strong, long-term wolves pressure on domestic animals (mainly sheep) (Gula, 2008).

Research from other systems does not show an increase in livestock depredation in relation to wild prey population declines (Sidorovich et al., 2017; Gervasi et al., 2020). We propose this may be because that given prey did not comprise a high enough proportion of wolf diet, or the prey population size did not fluctuate enough during the study to show an effect. Our results suggest that only a decrease in the number of more than 30% above the reference level could be correlated with the number of depredated livestock (Fig. 7). Thus, this would confirm the speculations of Mori et al. (2017) that heavy artificial reduction of wild boar numbers would intensify predation on roe deer and livestock. Consequently, disease outbreak and subsequent mitigation efforts of a secondary prey species may result in increased wolf-livestock depredation, human-wildlife conflict, and greater management challenges.

Perhaps the severity of livestock depredation in some regions could be explained by the historical dynamics of prey populations. We speculate that if there had been significant fluctuations in natural prey in the past, wolves may attack the livestock more often because they were once forced to survive the same way. This would be in line with the approach that wolves are more likely to kill livestock after an initial event of livestock depredation (Harper et al., 2008; Bradley et al., 2015). It should be noted, however, that studies in Estonia showed that after a significant decline in wild boar, there was a significant change in wolf diet, but towards alternative wild prey rather than livestock (Valdmann and Saarma, 2020). This suggests that other factors, such as wolf density, pack composition, and measures to minimize the wolf impact on livestock can also impact livestock depredation by wolves (e.g., Gehring

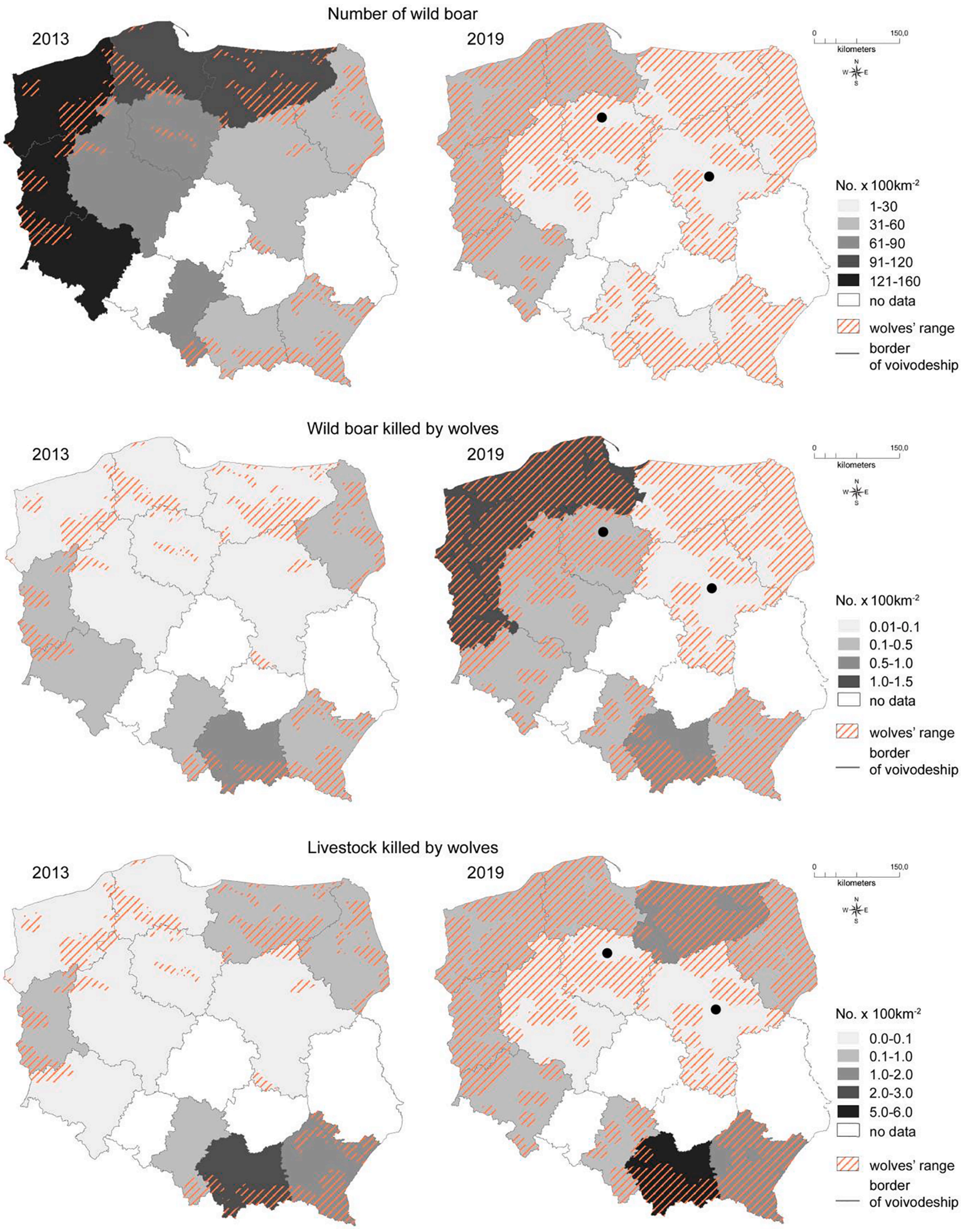

Fig. 4. The population size of wild boar, and number of wild boar and livestock killed by wolves in voivodeships in Poland in 2013 and 2019 (black dot marks the voivodeships for which we used data for 2018 instead 2019).

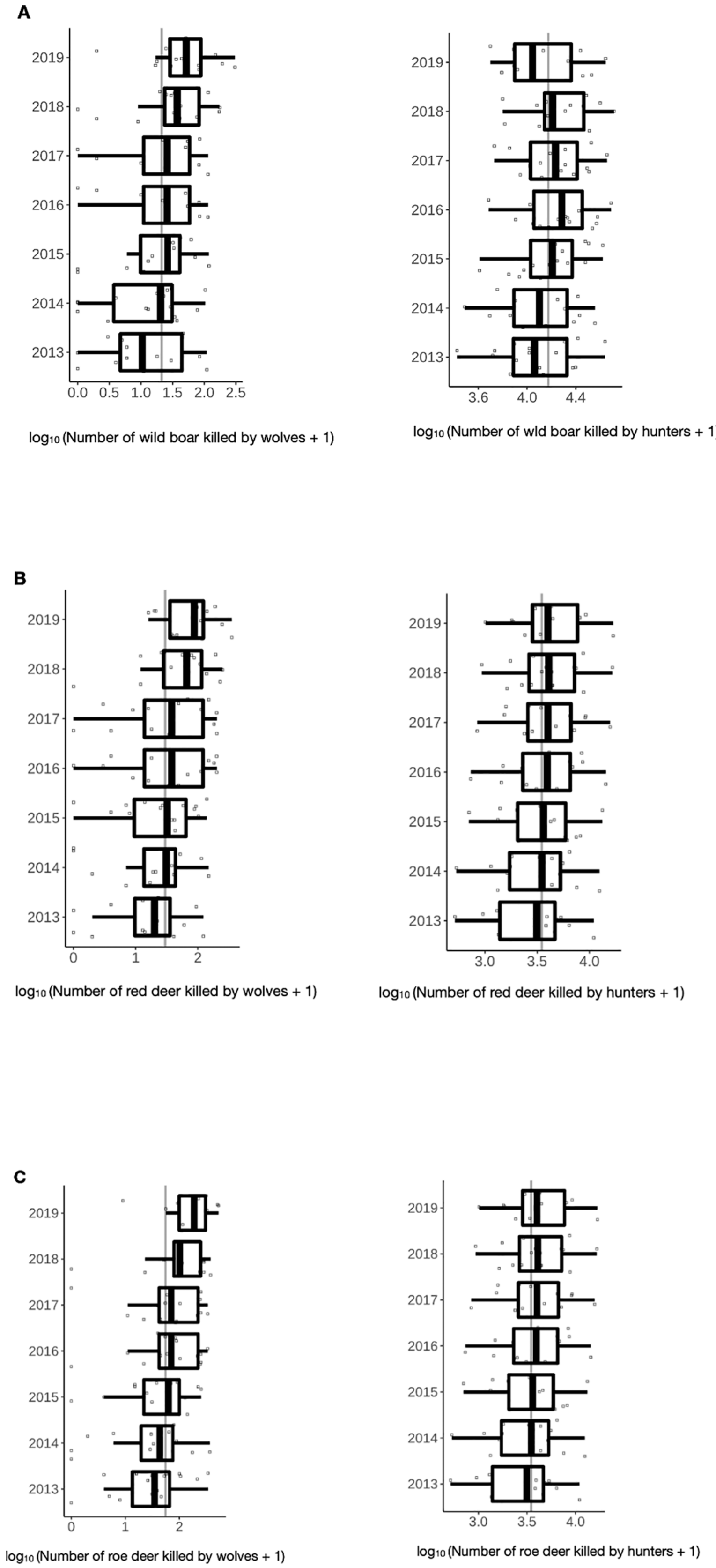

Fig. 5. Box plots showing the number of wild boar (A), red deer (B) and roe deer (C) killed by wolves (left panel) and hunted by hunters (right panel) between 2013 and 2019 across Poland. The X-axis shows log10-transformed fold change value of killed animals (wild boar, red deer and roe deer) by either wolves or hunters. The gray vertical line indicates the mean value for the study period. The gray points are the raw data used to generate the box plots.

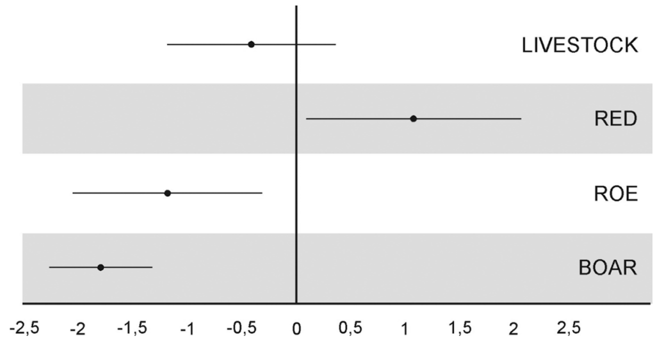

Fig. 6. Parameter estimates of livestock depredation by wolves in Poland between 2013 and 2019. Model averaged estimates of B coefficients and confidence intervals are taken from top models within ΔAICc < 2. Variables: BOAR – wild boar population numbers, ROE– roe deer population numbers, RED– red deer population numbers, LIVESTOCK – livestock numbers.

Table 1
Coefficients of intercept and wild boar population numbers for each voivodeship separately (for all a fixed coefficients were for RED: 0.89, ROE: −0.95 and LIVESTOCK: −0.59).

Voivodeship	Intercept	BOAR
Dolnośląskie	1.24	−2.27
Kujawsko-Pomorskie	0.61	−3.17
Lubuskie	1.19	−2.34
Małopolskie	2.54	−0.42
Mazowieckie	1.83	−1.43
Podkarpackie	2.21	−0.90
Podlaskie	1.74	−1.56
Pomorskie	1.48	−1.93
Śląskie	1.18	−2.35
Warmińsko-Mazurskie	1.96	−1.25
Wielkopolskie	1.62	−1.73
Zachodniopomorskie	1.40	−2.04

Table 2
Effect of wild boar population size on the number of roe deer and red deer killed by wolves (ΔAIC_c – difference in AIC_c values between the model with the variable and the null model). Parameters include BOAR – wild boar population numbers, ROE– roe deer population numbers, RED– red deer population numbers.

Model (dependent variable)	Source	*B*	Standard error	*p*	ΔAIC_c with the null model
ROE	Intercept	5.56	0.28	<0.001	23.5
	BOAR	−7809.5	1390.1	<0.001	
RED	Intercept	4.74	0.28	<0.001	12.2
	BOAR	−5367.9	1334.3	<0.001	

et al., 2011; Imbert et al., 2016; Santiago-Avila et al., 2018).

Our study suggests that the mechanisms driving wolf depredation on livestock are complex, as indicated in other studies (Eklund et al., 2017; Gervasi et al., 2020). This is indicated by the importance of roe deer in explaining the number of livestock depredation. However, that decreasing roe deer numbers was correlated to increased livestock depredation was probably a secondary effect. Roe deer are one of the species that compensate for the decline in the number of other ungulates in the wolf's diet (Gazzola et al., 2007; Mori et al., 2017; Valdmann and Saarma, 2020; Klich et al., 2021). This was confirmed in our study by a significant increase of killed roe deer with the decline of wild boar numbers (Table 2). Higher impact of wolves on roe deer probably caused the decline of roe deer numbers between 2017 and 2019, when the most drastic decline of wild boar appeared (Fig. 2).

More surprising was the positive relationship between livestock depredation and the number of red deer (Fig. 6). Red deer are the primary prey for wolves in Poland (Jędrzejewski et al., 2012) and thus we expected an increase in livestock depredation when red deer populations decreased, i.e., a negative relationship. However, the observed positive relationship was likely a statistical artifact due to correlation between livestock depredations and red deer distribution in Poland. Red deer were the most numerous in the northern and western voivodeships, where a greater amount of the livestock depredation occurred (Fig. 4). The wolf population in these regions was also the highest, and showed a greater increase during our study time frame (Fig. 4). It is probable that areas that had larger red deer populations facilitated wolf population growth, which resulted in an increased number of depredation incidents (i.e., more wolves implies more depredation).

It should also be noted that both red and roe deer populations grew between 2016 and 2017, the same time frame that marked the beginning of wild boar population decline. The reason could not be the lower impact of hunting by hunters, because harvest remained at a similar level as in the previous years, and even showed an upward trend during that time (Fig. 5B, C). The reason is also likely not due to foraging by wolves on wild boar killed by African swine fever, because red deer growth also occurred in voivodships where African swine fever was not found. This relationship suggests a potential link between the number of wild boar and the population size of both species of Cervidae. Red deer and roe deer are regarded as competitors (Bartos et al., 2002; Spitzer et al., 2021), but both species are not regarded as competitors of wild boar because they differ in diet from this species (Spitzer et al., 2020). Nevertheless, competition may arise in relation to supplementary feeding during winter. Supplementary feeding has a significant impact on wild boar diet (Ballari, and Barrios-García, 2014; Zeman et al., 2018), resulting in a higher a survival rate of young individuals in winter as well as earlier age at reproductive maturity (e.g., Geisser and Reyer, 2005; Merta et al., 2014). For deer, winter supplementary feeding seems to have a smaller impact, as a small amount of supplementary food was found in their diet (Katona et al., 2014). However, both roe and red deer willingly use winter supplementation (Arnold et al., 2018; Ossi et al., 2020), which effectively reduces agricultural damage caused by these species (Rajský et al., 2008; Borowski et al., 2019). Mátrai et al. (2013) showed that competition between red deer and wild boar for winter supplementary feeding was likely.

Our study also has practical relevance with regard to the management of wild animal populations and human-wildlife conflicts. The logistic regression model has shown that it is possible to predict the dramatic decline of prey that are not even primarily selected by the predator. This is important given that many ungulate populations are among the most threatened (Schipper et al., 2008), and current conservation measures have not brought the expected results (Hoffmann et al., 2010; Wolf and Ripple, 2016). Many ungulate species are monitored sporadically every few years (e.g., Klich and Magomedov, 2010; Easa and Alembath, 2018; Oladipo et al., 2019), and their conservation status is poorly known (Schipper et al., 2008). In some remote areas, estimation of wild ungulates is based on trophy hunting areas. This strategy allows for regular monitoring of ungulates subjected to moderate exploitation (e.g., Michel, 2008; Singh and Milner-Gulland, 2011; Valdez et al., 2016). Nevertheless, this approach is subject to criticism with regard to ethical, economic, and ecological effects (Lindsey et al., 2007; Nordbø et al., 2018; Batavia et al., 2019). In addition, the methods used in the monitoring of ungulates are burdened with a large error, which makes it difficult to determine the actual trends (Singh and Milner-Gulland, 2011). For this reason, monitoring of damage caused by predators can be a cheap alternative, or supplementation to, monitoring their prey abundance; i.e., monitoring livestock depredation patterns could provide important information about wild prey. More pronounced changes in the severity of livestock depredation could indicate a marked decline in the prey population.

Attention should be paid to the limitations of our study. The primary source of potential bias is the quality of the data, both of wolf and prey

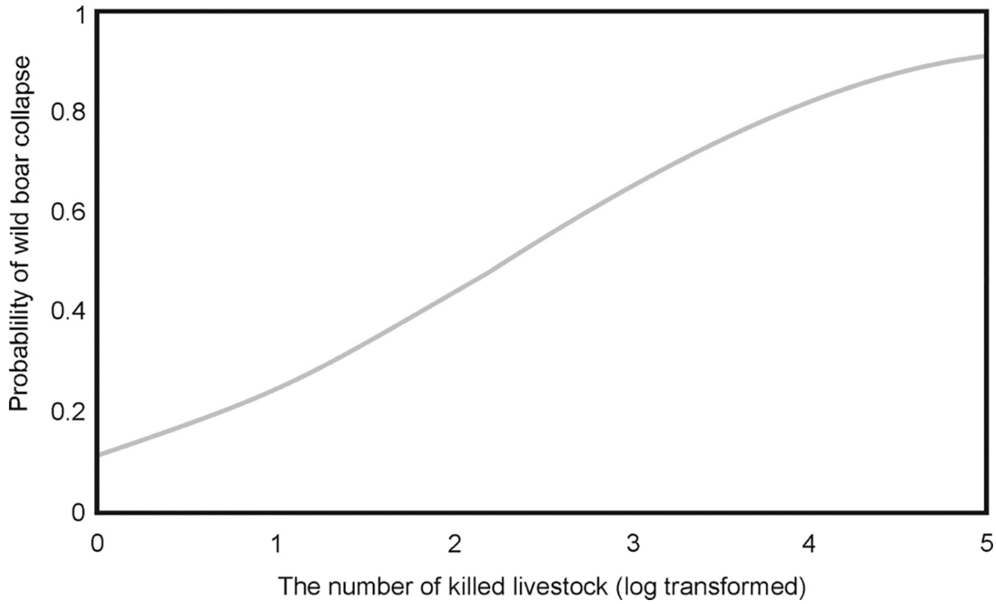

Fig. 7. Logistic response of the wild boar drastic decline (population size lower than 30% than the reference level) to the numbers of killed livestock (B_0 = -1.922 (±SE 0.665), z = -2.891, p = 0.004, $B_{killed\ livestock}$ = 0.863 (±SE 0.361), z = 2.394, p = 0.017, N = 65).

numbers. Data on the wolf population numbers are originated from the Central Statistical Office database, which is based on information from the Regional Directorates for Environmental Protection. Therefore, the data is uncertain. Similarly, the data on the number of wolves prey used, obtained from the Polish Hunting Association, are also erroneous estimations of populations sizes in hunting districts. Estimated data may have influenced our results. This is especially true of the effect of the wolf population on livestock depredation. The wolf population shows an upward trend in recent years in Poland. It should therefore be expected that this increase (wolves' population numbers) could contribute to the increase in the number of livestock attacks. However, no such dependence was shown in our models. Despite the above limitations, we believe that the trends we have demonstrated reflect real processes that, in our opinion, are logical and suggest that the proposed indicator may be applicable.

5. Conclusions

Our study shows that the nation-wide outbreak of African swine fever, and the subsequent mitigation efforts, triggered a cascade of changes in predator–prey relationships in Poland. The first effect was a decrease in the number of wild boar, which caused an increase in livestock depredation by wolves, but also increased wolves' hunting of alternative wild prey, roe deer and red deer. We presume that the Cervidae species benefited from the decline of wild boar numbers in the first period, as they showed an increase in numbers during a drastic decline in the wild boar population. This benefit, however, was short-lived as increased hunting of these species by wolves subsequently occurred. The changes in predator–prey relationships found in our study may be helpful in explaining the effect of livestock depredation. Our study confirms that clear changes in the number of prey can increase livestock depredation, while they may be undetectable when the changes in the numbers of natural prey are not very big. In our opinion, this indicates that the assessment of factors influencing livestock depredation should consider historical changes in prey dynamics.

Our study has also shown that it is possible to predict a drastic decline in wolf prey numbers (even with secondary prey) by the number of livestock killed by wolves. If our interpretation is correct, it provides a chance for managers and conservationists to use the predator population for indirect monitoring of prey species. Such monitoring could be used as a "first alert system" for ungulate populations. The occurrence of symptoms of more serious changes, i.e., a sudden increase wolf depredations across a large area, should trigger an alarm and prompt verification of the number of prey in the environment. Such a system would be inexpensive, and could be useful in the case of large, protected mammals not subject to monitoring, or under occasional monitoring. It could also serve as controls for field monitoring based on trophy hunting or any other ones. The main benefit could be the chance to prevent further undesirable changes in the number of ungulate populations monitored in this way. Moreover, in such a system, it is justified to maintain, not harass the predator population, which constitute the basic element of this system. Perhaps it would also increase the effectiveness of their protection.

CRediT authorship contribution statement

Daniel Klich: Conceptualization, Methodology, Formal analysis, Investigation, Visualization, Writing – original draft, Supervision. **Maria Sobczuk:** Conceptualization, Investigation, Writing – original draft. **Sayantani M. Basak:** Formal analysis, Visualization, Writing – original draft. **Izabela A. Wierzbowska:** Investigation, Writing – original draft. **Aimee Tallian:** Methodology, Writing – original draft. **Magdalena Hędrzak:** Investigation, Visualization, Writing – original draft. **Bartłomiej Popczyk:** Investigation, Writing – review & editing. **Krzysztof Żoch:** Conceptualization, Investigation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.108419.

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