



Article Does Wolf Management in Latvia Decrease Livestock Depredation? An Analysis of Available Data

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Abstract: In Latvia, livestock depredation by wolves has increased during the last two decades. Most of the attacks occur in summer and autumn during wolf hunting season. Use of effective preventive measures in Latvia is low, and farmers primarily rely on wolf hunting as a depredation reduction measure. The total numbers of wolf attacks and number of affected sheep per year in regional forest management units were analyzed in relation to the estimated wolf density, extent of culling, and proportion of juveniles, as well as the sheep density and estimated number of wild prey animals. The response variables (number of attacks and affected sheep per year) were modelled using a negative binomial regression, testing the effects of every covariate separately and building models from the significant covariates. The depredation level was related to sheep density and estimated wolf population size. No reducing effect was found for culling, and an even greater depredation rate was expected when the proportion of culled wolves increased. In addition, no significant effect was associated with the other covariates. However, greater numbers of affected sheep were expected at higher red deer density, suggesting increased opportunistic livestock depredation when red deer locally outcompete roe deer, the preferred wolf prey in Latvia.

Keywords: wolf; Canis lupus; livestock; depredation; Latvia

1. Introduction

For centuries humans have had diverse and complicated relationships with wolves [1], and livestock depredation is of the predominant sources of human–carnivore conflict [2,3]. Wolf attacks on livestock affect human attitudes towards them [2–5], leading to persecution and even complete eradication of this predator in many countries [1], even though more livestock are lost to diseases, harsh weather conditions, and other factors [2,6]. Due to the relatively recent recovery of wolf populations in many European countries [7] and increased depredation associated with prolonged livestock herding and breeding in the absence of wolves, derogation and more extensive application of lethal control is being reconsidered [8]. Mitigation of conflicts with wolves is important to ensure their conservation as an important part of the ecosystem, to maintain the habitual lifestyle and sources of income of local people, and to improve attitudes towards these carnivores [9–11].

Compared to other European countries, such as Sweden, Norway, Estonia, Poland, Slovenia, France, and Italy [2,12–16], livestock depredation by wolves in Latvia in the 21st century is rather low [17], with an average of 25 reported cases per year (varying from 9 to 79) [18], although it can cause significant damages to individual farmers. There are currently no subsidies for acquisition of preventive measures and no compensation paid for lost animals in Latvia [17]. As the wolf population is not endangered and wolves are hunted in Latvia, culling is seen as a management measure that can decrease the amount of livestock depredation. Lethal control of carnivore populations to reduce depredation



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Copyright: © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). and support the livestock industry is implemented in many countries [1,6,19]; however, the effectiveness of hunting is unclear, and has been questioned in some cases [9,10,20–23], as there are many factors (for example, lack of wild prey, number of wolves in the area, existence of wolves specializing in livestock depredation, social structure of the wolf population, stability of wolf packs, livestock density in the area, use of preventive measures, landscape characteristics) influencing the occurrence of depredation and the impact of hunting [9,13,14,19,20,24–26].

The aim of this study was to investigate the relationship between reported livestock depredation in Latvia and available data on the estimated density of wolves and their wild prey, as well as on culling from 2004 to 2022. Specifically, we searched for evidence of a negative impact of wolf hunting on the reported number of attacks and affected livestock to determine whether livestock depredation was locally minimized by wolf culling according to the implemented management approach. As wolf hunting can disrupt pack structure, and may cause juvenile individuals to resort to livestock depredation [19], we examined the relationship between livestock depredation and juvenile proportion, which was estimated according to the observed age structure among the culled individuals.

2. Materials and Methods

2.1. Wolves in Latvia

The study area, wolf management, and routine sampling of culled individuals in Latvia is described in more detail by Šuba et al. [27]. Wolves are distributed throughout the whole country [17,18]. A hunting season from 15 July until 31 March and a hunting quota were both introduced in Latvia in 2004. Before their implementation, wolves were hunted without any restrictions. The quota is set annually for the whole country, and the amount of livestock depredation is one of the considerations when deciding the size of the quota. The quota has been increased following its introduction, and for the last decade has been set to around 270–300 wolves per hunting season. In Latvia, the hunting pressure on wolves is rather high, with human-caused mortality estimated to be around 37% in the last two decades [27]. While the occurrence of illegal wolf hunting is plausible, its prevalence is unknown. The main prey species for wolves are roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), and to a lesser extent red deer (*Cervus elaphus*) and Eurasian beaver (*Castor fiber*) [17,28].

2.2. Data Acquisition and Preparation

The data we analyzed in this study, referring to a period from 2004 until 2022, were obtained from the Latvian State Forest Service (SFS) and the Agricultural Data Center via the Central Statistical Bureau of Latvia. The SFS conducts a game census and investigates reports on livestock depredation by wild carnivores, while the Agricultural Data Center compiles data on livestock numbers per statistical region annually. Reports to the SFS about cases of damage are voluntary, and as there is no compensation paid for losses, not every farmer reports occurrences of depredation. The amount of unreported cases is unknown. From all reported cases, we analyzed only wolf attacks. Although wolves can be determined as a culprit in attacks by stray dogs or bears, such cases should not be substantial. Bear attacks are usually rather distinct from wolf attacks, and an ongoing study on DNA analyses showed that in Latvia, stray dogs rarely cause damage to livestock. For example, in 156 DNA samples taken from livestock depredation victims between 2018 and 2022, the presence of wolf DNA was confirmed in 88.5% cases [29].

In this study, we focused on wolf attacks on sheep, which comprise 90% of all reported livestock depredation cases. The SFS data corresponding to ten regional forestry units (Figure 1) were published on the SFS website [18,30] or made available upon request. Reports on livestock depredation included the date, location, number of killed, injured and lost sheep, the circumstances of the attack, and the preventive measures applied. In this study, victims were pooled into a single category (i.e., affected sheep). Data on applied livestock protection measures at sites where depredation had occurred (n = 506) were

available for the years 2000–2020. The effectiveness of preventive measures was evaluated according to available recommendations [23,31–33].



Figure 1. Borders of local forestry units of the Latvian State Forest Service (red) and statistical regions (black).

Summary statistics on wolf attacks on sheep, wildlife abundance, and number of sheep in the SFS within the forestry units as well as the number of sheep in statistical regions, are provided in the Appendix A (Table A1). The estimated numbers of wolves, as well as red deer, roe dear, wild boar, and Eurasian beaver, provided by the SFS were used to account for wolf density and availability of wild prey. The number of culled wolves per forestry unit per year was used to account for hunting pressure. However, as this number was expected to correlate with estimated abundance, the culling intensity was expressed as the ratio between the number of culled individuals and the estimated number of wolves in the forestry unit.

Data on number of sheep in five statistical regions of Latvia (Figure 1) were used to account for regional variation in sheep density. A summary of sheep numbers from 2004 to 2022 is provided in the Appendix A (Table A2). As the borders of the statistical regions differ from the borders of the forestry units, data from individual or adjacent statistical regions corresponding to two to six neighboring forestry units within common or negligibly differing borders were pooled. The calculated number of sheep per km² refers to all the forestry units within the array. Data on wolf age structure from 2004 until 2021 were obtained by the authors following examination of legally culled individuals and otherwise found carcasses (see Šuba et al. [27] for more details). Tooth samples for age assessment were prepared according to the methods described by Klevezal [34]. Age was determined via microscopic inspection and counting the increment lines in a cross-section of the extracted canine. For the purposes of this study, age was assigned to three age classes, namely, juveniles (i.e., individuals born in spring prior to opening of the hunting season), subadults (individuals aged one year), and adults (individuals aged two years

and older). This allowed inclusion of adult individuals from which a tooth sample was unavailable and the precise age remained undetermined. In total, ages were recorded for 1902 individual wolves of known location. As the number of wolves with known age from individual forestry units per year was often insufficient for credible estimates, data from three to four neighboring forestry units were combined and the calculated proportion of juveniles among the sampled individuals was assigned to every forestry unit in the array.

2.3. Data Analysis

First, we obtained pooled information on reported livestock depredation cases and the number of affected sheep. In addition to the general description, the timing of attacks and the relationship with estimated wolf density within the country were analyzed. Afterwards, depredation cases within local forestry units were examined in relation to the available data.

The total number of reported attacks and affected sheep per year within a regional forestry unit were treated as response variables. Covariates are listed in Table A3 of the Appendix A and included nominal variables (i.e., taking value 0 or 1) which corresponded to forestry units and quantitative variables, namely, the mean number of sheep per 1 km², the estimated number of wolves, the proportion of juvenile wolves, the proportion of culled individuals in the current and previous year, and the abundance of prey species in the current and previous year. Estimated prey density was expressed in thousands. Proportional variables (i.e., the proportions of culled individuals and of juveniles) were transformed using a logit function, as this provided a more feasible range. In one case, this variable assumed a value of -7 below 0.1%, and in two cases above 100% the value of 7 was assigned, as slightly more individuals per forestry unit were culled than were estimated to be present.

The relationship between the number of attacks or affected sheep and the covariates was investigated by means of a negative binomial regression. All the models were based on the same 58 records of response variables (total numbers per year) and associated values of the covariates. Initially, the effects of each covariate on the response variables were tested separately, comparing the model containing an intercept and a single covariate with a null model using the likelihood ratio test. Then, models which contained combinations of significant covariates were compared to each other. The statistical analyses were conducted using R software [35], and the MASS package was applied.

3. Results

During the study period, both the number of reported and verified wolf attacks on livestock and the number of affected sheep have fluctuated considerably, showing a slightly increasing trend (Figure 2).

The mean number of affected sheep per reported attack increased from 2.6 (in 2004–2009) to 5.5 (in 2017–2022) with a slope of 0.219 (SE = 0.077) per year (Figure 3). This increase was found to be statistically significant (linear regression analysis, $F_{1,17} = 8.16$, p = 0.011).

No livestock protection measures were used in 181 (35.8%) reported depredation cases. In 266 (52.6%) cases, the applied preventive measures were considered as inappropriate (electric fences with only one or two wire lines; electric, wood, or barbed-wire fences less than 1 m high; chained guard dogs). Only ten (2%) farms on which depredation occurred used more effective preventive measures (e.g., a shepherd or appropriate electric fencing at least 1.2 m high with five or six wire lines or mesh weave). In 49 (9.7%) cases, the reports contained no information about the use of preventive measures.

While wolf attacks were reported throughout the year, the majority occurred in summer and autumn (Figure 4). As wolf hunting season begins on 15 July, in most years it covered the period in which the majority of the attacks were reported.



Figure 2. Number of reported wolf attacks and affected livestock (**a**) and number of affected (i.e., killed, injured, or lost) sheep per attack (**b**), showing minimum, maximum, median, inter-quartile range, and number of cases in Latvia from 2004 to 2022 (data from the Latvian State Forest Service).



Figure 3. Increase in mean number of affected sheep per reported wolf attack in Latvia from 2004 to 2022 (solid and dashed lines indicate the linear trend and 95% confidence intervals, respectively; data from the Latvian State Forest Service).



Figure 4. Timing of reported wolf attacks on livestock throughout the year (earliest, latest, median, inter-quartile range, and number of cases). Gray shading indicates period of closed hunting season for wolves.

Overall, the total number of wolf attacks and affected sheep increased with the estimated wolf density in the country (Figure 5), which was determined to be a significant factor according to negative binomial regression and likelihood ratio tests (for the number of the attacks, $\lambda_{LR} = 5.911$, df = 1, p = 0.015; for the number of affected sheep, $\lambda_{LR} = 20.849$, df = 1, p < 0.001). However, investigation at the level of SFS local forestry units revealed other relationships in which the estimated number of wolves no longer had such a significant effect.



Figure 5. Observed and predicted number of reported attacks by wolves (**a**) and number of affected sheep (**b**) per year according to estimated wolf density (the solid and dashed lines indicate the expected number and 95% confidence intervals according to a negative binomial regression, respectively; data from the Latvian State Forest Service).

By investigating the relationships between the number of wolf attacks on sheep and the available covariates via negative binomial regression, the local forestry unit ($\lambda_{LR} = 18.17$, df = 8, p = 0.02), mean number of sheep per km² ($\lambda_{LR} = 7.724$, df = 1, p = 0.005), and proportion of culled wolves in the current year ($\lambda_{LR} = 6.74$, df = 1, p = 0.009) had significant effects, while other covariates had no significant effect on the intercept (likelihood ratio tests, p > 0.05). The statistics of the negative binomial regression models containing combinations of these covariates and the estimated wolf density are provided in Appendix A (Table A4). However, the proportion of culled wolves had positive coefficient values, i.e., higher expected depredation rate, at a higher culling intensity. Other covariates, such as density

of other wildlife species and proportion of juveniles, had an insignificant effect on the total number of depredation cases according to likelihood ratio tests (p > 0.05). The mean number of sheep per km² had a significant effect on the cumulative number of affected sheep ($\lambda_{LR} = 6.616$, df = 1, p = 0.01). The most parsimonious models according to AIC values included the forestry unit and the estimated number of wolves and red deer among the factors (Table A5 of the Appendix A). Likelihood ratio tests revealed no significant effect of other covariates (p > 0.05).

4. Discussion

In Latvia, numbers of reported livestock depredation cases and affected sheep were correlated with estimated wolf density, as most farms (88.4%) where wolf attacks occurred applied no or insufficient preventive measures against such attacks. In a survey on public attitudes towards large carnivores [15], most livestock farmers (73.4%) claimed that they do not use any preventive measures. Wolf hunting was deemed an effective means of reducing depredation by 84.1% of surveyed farmers, and 41.1% of farmers considered hunters to be responsible for the prevention and reduction of wolf depredation. Only 29% of surveyed farmers claimed personal responsibility for the prevention of depredation cases. Generally, prevention was introduced only after loss of livestock had been suffered due to wolf attacks.

Most attacks were reported during summer and autumn. Similar timing of wolf attacks on livestock has been observed in other countries [1,4,12,13,15,24,36–39]. In Latvia, unlike in neighboring Estonia [16] and Lithuania [40], wolf hunting season begins considerably earlier, on 15 July compared to 1 November and 15 October, respectively, coinciding with the majority of the observed attacks on livestock. Nevertheless, we found no indication that wolf hunting in the current or following year decreased the reported number of attacks or the number of affected sheep in SFS local forestry units. On the contrary, significantly more attacks were expected in the current year with a higher ratio between the number of culled wolves and the estimated number of wolves, as the coefficient was positive and significantly different from zero. As seen in previous studies, lethal predator control can be less effective than other preventive measures [14,20,23], and appropriate livestock protection can be more significant than a reduction in wolf numbers in decreasing the number of depredation cases [32,41].

While hunting can have a short-term positive effect on depredation reduction, it does not prevent attacks in the long term, as harvested animals are soon replaced by dispersing individuals [24]. In fact, in certain cases wolf hunting can increase the amount of depredation [19,20,25], as hunting impacts the demographic, territorial, and social structure of wolf populations, leading to potentially higher reproduction rates [42] and possible changes in animal behavior, including hunting habits [19,43,44]. As wolf hunting in Latvia begins when pups are very young and will continue to depend on adult animals for their survival for some time [45], the loss of parents or other adult pack members may make it more difficult for the remaining adults to provide for the pups [44], and as a result they may choose more vulnerable prey, e.g., livestock.

Theoretically, an increase in livestock depredation may be associated with disrupted pack structure and accidental removal of adults due to intensive hunting [19]. However, our analysis revealed no significant relationship between the number of attacks or number affected sheep and the observed proportion of juvenile wolves. In fact, juveniles are more likely to be removed from the population due to hunting than adults [46]. Additionally, having an abundant wild prey base decreases the possibility of depredation by juvenile wolves. The impact of culling on wolf pack structure needs to be evaluated in further studies involving existing kinship data, as individual circumstances in packs, such as the juvenile's age when losing adult pack members or early dispersal from the natal pack, might be important factors leading juveniles to depredation.

Another significant factor influencing the number of reported depredation cases and affected sheep was the location in particular SFS forestry units. In addition to regional

variation of the analyzed covariates (Appendix A, Tables A1 and A2), local differences in the operation of the SFS and the activity of farmers in reporting cases may be relevant. However, qualitative or quantitative assessment of such characteristics is problematic.

No correlation was found between sheep depredation and the estimated numbers of most prey species. Although the numbers of roe deer and wild boar in Latvia have fluctuated [17,27,47], there is no reason to assume significant shortages at any point. However, the number of affected sheep was related to estimated numbers of red deer, and according to estimated coefficients, more affected sheep were expected at higher red deer densities. This may be associated with competition between the two deer species [48,49], as roe deer are more common in the wolf diet in Latvia [28], and may be affected by higher red deer density increasing opportunistic livestock depredation. In Europe, red deer are preferred in the wolf diet [50]; however, hunting them may require advanced hunting skills or greater pack size.

In Latvian society, various opinions exist concerning wolves [51,52]. Generally, livestock farmers and herders are the most negative in their attitudes towards wolves [53–59], as their income and lifestyle are affected by depredation. In addition, the wolf is sometimes seen as a symbol of the domination of the urban population over the lifestyle and needs of rural inhabitants. Therefore, negative attitudes towards this carnivore may originate from the symbolic meaning of the animal and general social and economic factors rather than from negative personal experiences with wolves [60,61]. Although it is often considered that attitudes should be improved in order to improve species conservation condition, in the case of livestock depredation practical measures that ensure successful coexistence may be of greater importance. The ability to accept the presence of wolves and coexist with them may be more important than engendering a positive attitude towards these carnivores. Acknowledgement of existing conflicts, hearing out of farmers and their problems, objective evaluation of the situation, and practical solutions for conflict mitigation might be more successful than attempts to improve knowledge and attitudes towards predators [62].

5. Conclusions

In Latvia, where the wolf population is not endangered and wolf culling is permitted, their lethal control is regarded as means of reducing livestock depredation. Nevertheless, as seen from this study, current wolf hunting practices in Latvia might not have the desired positive effect on depredation reduction. To minimize livestock depredation, improvements in applied livestock depredation measures must be considered rather than increasing culling quotas. Thus, the use of effective preventive measures and subsidies for their implementation are significant approaches in the context of sustainable coexistence with these carnivores.

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Appendix A. Summary of Analyzed Data

Table A1. Summary statistics (minimum, maximum, and median values per year) on wolf attacks on sheep and applied wildlife data of Latvian State Forest Service local forestry units (Figure 1) from 2004 to 2022.

	Dienvidkurzeme	Ziemeļkurzeme	Zemgale	Rīga Regional
Reported wolf attacks on sheep	1–9 (3)	1–8 (3)	5 1-4 (1)	
Total number of affected sheep	1-61 (20)	1–50 (17.5)	26 1–24 (12.5)	
Estimated number of wolves	95–337 (169)	77-260 (158)	11-129 (88)	5-45 (14)
Number of culled wolves	20-42 (28)	17–55 (39)	3–39 (14)	1–11 (5)
	175 juv	163 juv	85 juv	26 juv
Age structure	30 subad	36 subad	11 subad	4 subad
Estimated numbers of other wildlife (thousands)	red deer 4.9–14.3 (10.8) roe deer 13.4–38 (22.4) wild boars 2.4–12.7 (7.2) beavers 4.9–13 (7.7)	red deer 6.6–13.6 (10.6) roe deer 7.3–22.6 (9) wild boars 1.2–11.4 (6.1) beavers 3.0–8.4 (4.0)	red deer 1.9–13.9 (10.2) roe deer 13.6–27.4 (22.9) wild boars 2.3–11.1 (4.0) beavers 3.4–12.3 (7.0)	red deer 1.3-4.3 (2.0) roe deer 8.9–28.9 (17.4) wild boars 0.8–5.8 (2.3) beavers 4.1–10.6 (5.7)
	Sēlija	Dienvidlatgale	Austrur	nlatgale
Reported wolf attacks on sheep	1–6 (1)	1–12 (2)	1–11	(3.5)
Total number of affected sheep	1–31 (11)	7–68 (12)	2–58	(16)
Estimated number of wolves	63–190 (151)	39–189 (124)	68–18	0 (99)
Number of culled wolves	5-37 (22)	4-36 (15)	6–53 (20)	
Age structure	101 juv 24 subad 82 ad	50 juv 10 subad 45 ad	57 juv 6 subad 56 ad	
Estimated numbers of other wildlife (thousands)	red deer 2.2–7.7 (5.2) roe deer 11.1–28.3 (18.4) wild boars 1.6–7.5 (3.7) beavers 2–7.7 (6.6)	red deer 0.5–3.1 (1.4) roe deer 10.1–25.4 (16.5) wild boars 1.9–5.9 (3.0) beavers 7.9–13.0 (11.6)	red deer 0.2–1.8 (0.7) roe deer 9.2–15.1 (12.2) wild boars 1.3–4.3 (2.7) beavers 6.2-8.6 (7.3)	
	Centrālvidzeme	Ziemeļvidzeme	Ziemeļa	ustrumi
Reported wolf attacks on sheep	1–28 (2)	1–9 (3.5)	1-9 (1)	
Total number of affected sheep	1–277 (14)	3–76 (27)	2–62 (5)	
Estimated number of wolves	11–205 (61)	41–143 (79)	33–169 (70)	
Number of culled wolves	4-47 (19)	2–42 (28)	3–45 (19)	
Age structure	71 juv 15 subad 68 ad	139 juv 17 subad 73 ad	103 juv 10 subad 65 ad	
Estimated numbers of other wildlife (thousands)	red deer 1–7.2 (4.5) roe deer 8.9–21.5 (13.5) wild boars 2.4–7.3 (4.2) beavers 5.0–8.9 (6.4)	red deer 1.5–4.7 (3.7) roe deer 12.6–41.2 (20.1) wild boars 1.1–10 (4.4) beavers 5.4–11.9 (6.5)	red deer 0.7–5.1 (2.7) roe deer 6.1–23.3 (10.0) wild boars 1.0–6.3 (2.6) beavers 4.1-8.4 (4.9)	

Table A2. Summary statistics on minimum, maximum, and median number of sheep in five Latvian statistical regions (Figure 1) from 2004 to 2022.

	Kurzeme	Zemgale	Pierīga	Vidzeme	Latgale
Non-urban area (km ²)	12,995	10,678	8562	15,750	14,463
Number of sheep (thousands)	4.4–19.0 (12.9)	2.0–14.6 (10.7)	3.8–17.8 (11.8)	7.0–33.5 (23.1)	20.0–28.5 (26.3)

Table A3. Investigated variables and coefficients corresponding to sheep depredation by wolves and available data.

Constant or Variable	Coefficient
Cumulative number of wolf attacks on sheep per year	1
Cumulative number of affected sheep in wolf attacks per year	1
Intercept	β _{int}
Centrālvidzeme SFS forestry unit	β _{forestry} [CV]
Dienvidkurzeme SFS forestry unit	β _{forestry} [DK]
Dienvidlatgale SFS forestry unit	β _{forestry} [DL]
Rīga Regional SFS forestry unit	$\beta_{forestry[RR]}$
Sēlija SFS forestry unit	β _{forestry} [S]
Ziemeļaustrumi SFS forestry unit	β _{forestry[ZA]}
Ziemeļkurzeme SFS forestry unit	β _{forestry} [ZK]
Ziemeļvidzeme SFS forestry unit	$\beta_{forestry[ZV]}$
Mean number of sheep per 1 km ² in respective region	β_{sheep}
Estimated number of red deer in current year in current year (in thousands)	$\beta_{wild[redd]}$
Estimated number of roe deer in current year in current year (in thousands)	$\beta_{wild[roed]}$
Estimated number of wild boars in current year in current year (in thousands)	β_{wild} [wildb]
Estimated number of beavers in current year in current year (in thousands)	$\beta_{wild[beav]}$
Estimated number of red deer in previous year in previous year (in thousands)	$\beta_{prevwild[redd]}$
Estimated number of roe deer in previous year in previous year (in thousands)	$\beta_{prevwild[roed]}$
Estimated number of wild boars in previous year in previous year (in thousands)	$\beta_{prevwild}$ [wildb]
Estimated number of beavers in previous year in previous year (in thousands)	β <i>prevwild</i> [beav]
Estimated number of wolves in current year	β_{wolf}
Logit-transformed proportion of culled wolves in current year	β_{wcull}
Logit-transformed proportion of culled wolves in previous year	β _{prevwcull}
Logit-transformed proportion of juvenile wolves in current year	β_{wjuv}

Table A4. Coefficients and statistics of investigated negative binomial regression models (overdispersion parameter, adjusted Akaike information criterion, difference, Akaike weight, and evidence ratio) describing cumulative number of wolf attacks on sheep per year in SFS local forestry units. Significant coefficients indicated by asterisks (*—p < 0.05, **—p < 0.01, ***—p < 0.001).

Coefficients (±SE)	θ (±SE)	AIC _c	Δ	ω	ER
$ \begin{aligned} \beta_{int} &= 0.742 \ (\pm 0.366) \ ^* \\ \beta_{sheep} &= 0.442 \ (\pm 0.195) \ ^* \\ \beta_{wcull} &= 0.263 \ (\pm 0.124) \ ^* \end{aligned} $	5.96 (±3.07)	243.65	0	0.562	1
$\beta_{int} = 0.293 \ (\pm 0.316)$ $\beta_{sheep} = 0.55 \ (\pm 0.196) \ **$	5.13 (±2.44)	245.39	1.73	0.236	2.4
$\beta_{int} = 1.501 \ (\pm 0.163)^{***}$ $\beta_{wcull} = 0.345 \ (\pm 0.125)^{**}$	4.71 (±2.09)	246.37	2.71	0.145	3.9
$ \begin{split} \beta_{int} &= 0.999 \; (\pm 0.374)^{**} \\ \beta_{forestry}[\text{CV}] &= -0.304 \; (\pm 0.376) \\ \beta_{forestry}[\text{DK}] &= -1.086 \; (\pm 0.368) \;^{**} \\ \beta_{forestry}[\text{DL}] &= -1.279 \; (\pm 0.391) \;^{**} \\ \beta_{forestry}[\text{RR}] &= -1.234 \; (\pm 0.669) \\ \beta_{forestry}[\text{S}] &= -0.858 \; (\pm 0.335) \;^{*} \\ \beta_{forestry}[\text{ZA}] &= -0.824 \; (\pm 0.351) \;^{**} \\ \beta_{forestry}[\text{ZK}] &= -1.173 \; (\pm 0.377) \;^{**} \\ \beta_{forestry}[\text{ZV}] &= -0.099 \; (\pm 0.28) \\ \beta_{wolf} &= 0.007 \; (\pm 0.003) \;^{**} \end{split} $	12.6 (±11.0)	250.02	6.37	0.023	24.1
$\beta_{int} = 1.127 \ (\pm 0.101)^{***}$	3.81 (±1.52)	250.96	7.31	0.015	38.6
$\begin{array}{l} \beta_{int} = 0.826 \ (\pm 0.496) \\ \beta_{forestry[CV]} = -0.545 \ (\pm 0.367) \\ \beta_{forestry[DK]} = -0.128 \ (\pm 0.393) \\ \beta_{forestry[DL]} = -0.867 \ (\pm 0.39)^* \\ \beta_{forestry[RR]} = -1.436 \ (\pm 0.638)^* \\ \beta_{forestry[S]} = -0.489 \ (\pm 0.342) \\ \beta_{forestry[ZA]} = -0.84 \ (\pm 0.34)^* \\ \beta_{forestry[ZK]} = -0.359 \ (\pm 0.352) \\ \beta_{forestry[ZV]} = -0.14 \ (\pm 0.276) \\ \beta_{sheep} = 0.539 \ (\pm 0.225)^* \\ \beta_{wcull} = 0.113 \ (\pm 0.135) \end{array}$	14.5 (±14.3)	252.52	8.87	0.012	46.4
$ \begin{split} \beta_{int} &= 1.735 \ (\pm 0.221)^{***} \\ \beta_{forestry[CV]} &= -0.482 \ (\pm 0.387) \\ \beta_{forestry[DK]} &= -0.736 \ (\pm 0.344)^{*} \\ \beta_{forestry[DL]} &= -1.042 \ (\pm 0.389)^{**} \\ \beta_{forestry[RR]} &= -1.735 \ (\pm 0.649)^{**} \\ \beta_{forestry[S]} &= -0.79 \ (\pm 0.348)^{*} \\ \beta_{forestry[ZA]} &= -1.042 \ (\pm 0.355)^{**} \\ \beta_{forestry[ZK]} &= -0.736 \ (\pm 0.344)^{*} \\ \beta_{forestry[ZV]} &= -0.253 \ (\pm 0.289) \end{split} $	8.58 (±5.69)	252.47	8.82	0.007	82.1

Table A5. Coefficients and statistics of negative binomial regression models (overdispersion parameter, adjusted Akaike information criterion, difference, Akaike weight, and evidence ratio) describing cumulative number of affected sheep in wolf attacks per year in SFS local forestry units. Significant coefficients indicated by asterisks (*—p < 0.05, **—p < 0.01, ***—p < 0.001).

Coefficients (±SE)	θ (±SE)	AIC _c	Δ	ω	ER
$ \begin{array}{l} \beta_{int} = 1.486 \ (\pm 0.41) \ ^{***} \\ \beta_{sheep} = 0.833 \ (\pm 0.226) \ ^{***} \\ \beta_{wild} \ [redd] = 0.075 \ (\pm 0.031) \ ^{*} \end{array} $	1.505 (±0.287)	474.97	0	0.423	1
$ \begin{array}{l} \beta_{int} = 1.564 \; (\pm 0.42) \; ^{***} \\ \beta_{sheep} = 0.674 \; (\pm 0.221) \; ^{**} \\ \beta_{wolf} = 0.005 \; (\pm 0.002) \; ^{*} \end{array} $	1.462 (±0.277)	476.68	1.71	0.18	2.4
$ \beta_{int} = 1.414 (\pm 0.427) *** \beta_{sheep} = 0.798 (\pm 0.233) *** \beta_{wild[redd]} = 0.06 (\pm 0.041) \beta_{wolf} = 0.002 (\pm 0.003) $	1.512 (±0.289)	476.98	2.01	0.155	2.7
$\beta_{int} = 2.128 \ (\pm 0.349) *** \beta_{sheep} = 0.65 \ (\pm 0.226) **$	1.379 (±0.259)	478.07	3.09	0.09	4.7
$ \begin{array}{l} \beta_{int} = 2.982 \ (\pm 0.311) \ ^{***} \\ \beta_{forestry}[\text{CV}] = -1.048 \ (\pm 0.586) \\ \beta_{forestry}[\text{DK}] = -3.085 \ (\pm 0.778) \ ^{***} \\ \beta_{forestry}[\text{DL}] = -0.521 \ (\pm 0.438) \\ \beta_{forestry}[\text{RR}] = -1.419 \ (\pm 0.56) \ ^{*} \\ \beta_{forestry}[\text{SI}] = -1.366 \ (\pm 0.504) \ ^{**} \\ \beta_{forestry}[\text{ZA}] = -1.585 \ (\pm 0.438) \ ^{***} \\ \beta_{forestry}[\text{ZK}] = -3.389 \ (\pm 0.934) \ ^{***} \\ \beta_{forestry}[\text{ZV}] = -0.547 \ (\pm 0.442) \\ \beta_{wild}[\text{redd}] = 0.311 \ (\pm 0.078) \ ^{***} \end{array} $	1.922 (±0.386)	478.94	3.97	0.058	7.3
$\begin{array}{l} \beta_{int} = 2.291 \ (\pm 0.463)^{***} \\ \beta_{forestry[CV]} = -0.449 \ (\pm 0.634) \\ \beta_{forestry[DK]} = -2.657 \ (\pm 0.78)^{***} \\ \beta_{forestry[DL]} = -0.632 \ (\pm 0.439) \\ \beta_{forestry[RR]} = -0.826 \ (\pm 0.629) \\ \beta_{forestry[S]} = -0.99 \ (\pm 0.507) \\ \beta_{forestry[ZA]} = -1.21 \ (\pm 0.465)^{**} \\ \beta_{forestry[ZK]} = -2.86 \ (\pm 0.938)^{**} \\ \beta_{forestry[ZV]} = -0.111 \ (\pm 0.473) \\ \beta_{wild}[red] = 0.225 \ (\pm 0.087)^{**} \\ \beta_{wolf} = 0.007 \ (\pm 0.004) \end{array}$	2.026 (±0.411)	479.05	4.07	0.055	7.7
$\begin{array}{l} \beta_{int} = 1.988 \ (\pm 0.465)^{***} \\ \beta_{forestry[CV]} = 0.712 \ (\pm 0.497) \\ \beta_{forestry[DK]} = -0.894 \ (\pm 0.461) \\ \beta_{forestry[DL]} = -0.602 \ (\pm 0.458) \\ \beta_{forestry[RR]} = -0.264 \ (\pm 0.611) \\ \beta_{forestry[S]} = -0.246 \ (\pm 0.428) \\ \beta_{forestry[ZA]} = -0.606 \ (\pm 0.435) \\ \beta_{forestry[ZK]} = -0.697 \ (\pm 0.475) \\ \beta_{forestry[ZV]} = 0.658 \ (\pm 0.4) \\ \beta_{wolf} = 0.011 \ (\pm 0.003)^{***} \end{array}$	1.85 (±0.37)	481.36	6.39	0.017	24.4

Coefficients (\pm SE)	θ (±SE)	AIC _c	Δ	ω	ER
$\begin{split} \beta_{int} &= 2.404 \ (\pm 0.618)^{***} \\ \beta_{forestry[CV]} &= -0.489 \ (\pm 0.646) \\ \beta_{forestry[DK]} &= -2.851 \ (\pm 1.08)^{**} \\ \beta_{forestry[DL]} &= -0.654 \ (\pm 0.455) \\ \beta_{forestry[RR]} &= -0.875 \ (\pm 0.636) \\ \beta_{forestry[S]} &= -1.082 \ (\pm 0.599) \\ \beta_{forestry[ZA]} &= -1.254 \ (\pm 0.486)^{**} \\ \beta_{forestry[ZK]} &= -3.046 \ (\pm 1.198)^{*} \\ \beta_{forestry[ZV]} &= -0.15 \ (\pm 0.508) \\ \beta_{sheep} &= -0.08 \ (\pm 0.321) \\ \beta_{wild[redd]} &= 0.237 \ (\pm 0.096)^{*} \\ \beta_{wolf} &= 0.007 \ (\pm 0.004) \end{split}$	2.025 (±0.411)	482.19	7.22	0.011	36.9
$\beta_{int} = 3.114 \ (\pm 0.121)^{***}$	1.241 (±0.228)	482.53	7.56	0.01	43.8

Table A5. Cont.

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