Does abundant wild prey decrease the risk of wolf damages in sheep farms in Finland?

Ilpo Kojola^{1,*}, Ville Hallikainen¹, Vesa Nivala¹, Samuli Heikkinen², Esa Huhta¹, Leena Ruha² & Jyrki Pusenius³

¹⁾ Natural Resources Institute Finland (Luke), Ounasjoentie 6, FI-96200 Rovaniemi, Finland (*corresponding author's e-mail ext.ilpo.kojola@luke.fi)

²⁾ Natural Resources Institute Finland (Luke), Paavo Havaksentie 3, FI-90570 Oulu, Finland

³⁾ Natural Resources Institute Finland (Luke), Yliopistonkatu 6, FI-80130 Joensuu, Finland

Received 30 Jan. 2024, final version received 21 Feb. 2025, accepted 21 Feb. 2025

Kojola, I., Hallikainen, V., Nivala, V., Heikkinen, S., Huhta, E., Ruha, L. & Pusenius, J. 2025: Does abundant wild prey decrease the risk of wolf damages in sheep farms in Finland?. — *Ann. Zool. Fennici* 62: 43–50.

Wild ungulates are the main prey of wolves in Finland. In theory, abundant wild ungulate populations could reduce the need for wolves (*Canis lupus*) to prey on livestock, as well as attract predators to the area. We tested the prey scarcity hypothesis by examining whether the number of sheep depredation cases in Finnish wolf territories was related to the population densities of moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), roe deer (*Capreolus capreolus*), or to the combined density of these ungulates. The absolute number of sheep depredation cases increased with the number of sheep farms, but was independent of the size of the wolf territories. Our statistical models suggested that the number of wolf attacks on sheep was negatively correlated with moose density, and also to some degree with roe deer density. White-tailed deer density and ungulate biomass did not explain numbers of wolf predatory attacks. The observed patterns could be explained by differences in the use of space by wild ungulates in relation to human settlements and sheep farms associated with those settlements; as in Finland, moose is the only ungulate that has been found to avoid human settlements.

Introduction

Grey wolves (*Canis lupus*) have recently increased in Europe in numbers, resulting in their expansion into human-dominated land-scapes where they are in conflict with anthropogenic activities (Piscopo *et al.* 2021), in particular by causing damage to livestock (Pimenta *et al.* 2018, Bruns *et al.* 2020, Cervasi *et al.* 2021, Janeiro-Otero *et al.* 2023). Protection measures

can reduce damage to livestock (Burns *et al.* 2020), but biological environment can also influence the risk of damage caused by predators (Cervasi *et al.* 2021, Mayer *et al.* 2022). The latter could be realized through a potential effect the abundance of wild prey populations may have on the level of damage caused by carnivores. The prey scarcity hypothesis suggests that low densities of wild prey may increase predation rates on livestock (Meriggi *et al.* 1996, Cervasi

et al. 2014, Khorozyan *et al.* 2015, Janeiro-Otero *et al.* 2020). On the other hand, when the spatial distribution of livestock and wild prey overlap, predator–livestock encounter rates can be higher in locations also used by wild prey (Treves 2004, Bradley & Pletcher 2005, Nelson *et al.* 2016). This is consistent with predictions based on the prey-tracking hypothesis (Nelson *et al.* 2016). These two hypotheses are not mutually exclusive. The prey scarcity hypothesis considers the abundance of wild prey at larger geographic scales, such as the size of wolf home ranges (Kojola *et al.* 2023), whereas the prey–tracking hypothesis considers spatial patterns of prey occurrence.

According to Cervasi *et al.* (2021), co-adaptation of large carnivores and humans is an integral part of ecology of the former. The grey wolf is probably the most controversial large carnivore species in Europe. It is a generalist predator with high reproductive and dispersal capabilities (Wabakken *et al.* 2001, Linnell *et al.* 2005, Wabakken *et al.* 2007, Kojola *et al.* 2009). Throughout their wide distribution, wolves prey on livestock, particularly sheep (Pimenta *et al.* 2018, Cervasi *et al.* 2021).

We investigated damages caused by resident wolves to Finnish sheep farms located within wolf territories with varying densities of natural prey. We estimated the effects of the population density of the three most abundant wild ungulates in wolf territories on wolf attacks on sheep. The prey scarcity hypothesis predicts a low risk of wolf predation on sheep in areas with high densities of wild ungulates. The prey-tracking hypothesis does not take into account the abundance of wild ungulates, but predicts that wolves that track wild ungulates may encounter sheep more often if wild ungulates share grazing areas with sheep. In discussing the results, we considered various distributional patterns and processes that could explain our findings beyond these particular hypotheses.

Material and methods

Wolves

Annual wolf territory boundaries (Fig. 1) were inferred from (1) point observations of packs and pairs based on approx. 2000 encounters reported by volunteers, (2) locations of GPS-collared territorial wolves, and (3) non-invasive genetic analyses used to separate neighboring packs and pairs from each other (Kojola *et al.* 2018).

Territory status (family pack or territorial pair) and numbers of wolves occupying each territory were assessed from the three data sets and known mortality rates by experts for the winters of 2016/2017 and 2017/2018 (Kojola *et al.* 2018), as well as using a Bayesian state–space model for the winters of 2018/2019 and 2019/2020 (Mäntyniemi *et al.* 2022).

Wild ungulate prey abundance

Wild ungulates are the main prey of wolves in northern Europe. Overall, moose (*Alces alces*) are the most important prey species, but deer can also become significant prey when they are abundant (Olsson *et al.* 1997, Gade-Jörgensen & Stagegaard 2000, Kojola *et al.* 2004, Ståhlberg *et al.* 2017). In our study, we used the following prey species density measures: (1) population density of moose (*Alces alces*), (2) population density of white-tailed deer (*Odocoileus virginianus*), (3) population density of roe deer (*Capreolus capreolus*), and (4) total density of ungulates (the three species taken together).

Moose population densities were calculated from estimates provided by hunters after the winter season. Population densities of white-tailed deer were based on estimates provided by moose hunters and originated from their moose hunting areas. Hunters also reported density estimates for roe deer from their hunting areas, but those were not official post-hunting estimates. Moose densities varied less among wolf territories than did densities of the roe deer and especially whitetailed deer. The white-tailed deer was highly concentrated in the south-western wolf territories (see Kojola et al. 2023: fig. 2). Moose were present in almost all study areas (see Kojola et al. 2023: fig. 2). Compared with white-tailed deer, roe deer were more evenly distributed in western Finland (see Kojola et al. 2023: fig. 2). Only moose density was normally distributed in wolf territories (see Kojola et al. 2023: fig. 2). The mean density of moose was about 3 indiv. 1000 ha-1. The density distributions of white-tailed deer and roe deer



Fig. 1. Wolf territories (red) and wolf attacks on sheep (blue dots) in Finland.

were skewed (*see* Kojola *et al.* 2023: fig. 2), as these species were absent from most territories in eastern Finland (*see* Kojola *et al.* 2023: fig. 2).

Sheep and wolf attacks on sheep

Locations of sheep farms were extracted from the farm register. There are about 1300 sheep farms with 131 000 sheep in Finland (see https://lammasyhdistys.fi/en/association/). Most of them are located in our study area. In Finland, about 90% of sheep are kept in fenced areas. Information on wolf attacks on sheep was obtained from the wildlife damage register (https://mmm.fi/riista/ riistavahingot). We analysed cases that took place between the beginning of June 2016 and the end of February 2020. We excluded wolf attacks that occurred in April and May because most wolves born in the previous year leave their natal territory by the end of April (Kojola et al. 2006), making it impossible to estimate the number of wolves occupying the territory during these months. This conclusion was based on movement data from 29 pups collared in winter (Kojola et al. 2006).

Statistical analysis

A generalised linear mixed models with negative binomial distribution assumption and log-link

function were constructed to model the count response (number of cases of wolves killing sheep in territory *i*). The model comprised two levels: wolf territory as the top level and years nested within territories. The number of years varied between territories and no serious temporal autocorrelations were found between neighbouring years. Therefore, the residuals could be treated as uncorrelated. The models were fitted using the R package *glmmTMB* (Brooks *et al.* 2017).

Two variance functions were tested using the R function *glmmTMB*: NB1 variance = $\mu(1 + \alpha)$ and NB2 variance = $\mu(1 + \mu/\theta)$ (Brooks *et al.* 2017). The NB1 parametrization suggested a linear mean-variance relationship, while the NB2 parametrization suggested a quadratic relationship. Both parametrizations gave almost the same AIC values for the models. The NB2 parametrization was used in the models, and the dispersion parameters of the NB2 models were used in the model fit simulations, giving directly the θ parameter for the simulations estimated using the R function *dnbinom*.

The R package *glmmTMB* also allowed zeroinflation modelling, but zero-inflation was not an obvious problem in the data. We tested it using the R package *DHRMa* (https://CRAN.Rproject.org/package=DHARMa). The results indicated that the negative binomial distribution worked without a zero-inflation coefficient in all models. The p values for the zero-inflation tests (function *testZeroInflation*) were clearly greater than 0.05. The test compares the number of simulated zeros (function simulateResiduals) with the observed ones.

The variance inflation factor (VIF) was used to check for possible multicollinearity of the main effects of the explanatory variables. The VIF was calculated using the R package *performance* (Lüdecke *et al.* 2021) and its function *check_collinearity*. Predictions with standard errors were computed using the R package *ggeffects* (Lüdecke 2018), and plots were made using the R package *ggplot2* (Wickham 2016).

All candidate models included the estimated number of wolves and the number of sheep farms in wolf territory, and the size of wolf territory. Model-specific variables for prey abundance were (1) moose population density, (2) white-tailed deer population density, (3) roe deer population density, and (4) total ungulate density. All candidate models included territory status (pair/pack). We assessed model fits using the Akaike information criterion (AIC) (Burnham & Anderson 2002). Models with Δ AIC < 2 were considered equally competitive.

Results

The number of depredation cases was negatively correlated to the population density of moose within the wolf territory (Table 1 and Fig. 2). However, the model with moose density and number of sheep farms as independent variables was only marginally better than the model in which moose density was compensated for by roe-deer density (Table 1). The number of depredation cases did not correlate with the population density of roe deer (Table 1 and Fig. 2).

The number of depredation cases increased with increasing number of sheep farms in models

Table	1. Parameters	used in gene	ralized linear	mixed models	s with nega	tive binomia.	l distribution	assumption f	ior the
numbe	er of cases in v	vhich sheep w	vere killed by	wolves.					

	Estimate	SE	Ζ	p	VIF
Model 1 (AIC = 243.4, <i>R</i> ² = 0.146)					
Intercept	0.136	1.233	0.110	0.912	-
Number of sheep farms in territory	0.063	0.028	2.111	0.035	1.60
Wolf number	-0.095	0.130	-0.736	0.462	1.11
Moose density (indiv. 1000 ha-1)	-0.628	0.304	-2.069	0.039	1.72
Variance in territory	0.589				
Residual df	177				
Model 2 (AIC = 247.6, R ² = 0.034)					
Intercept	-1.994	-0.869	-2.295	0.022	-
Number of sheep farms in territory	0.032	0.030	1.073	0.283	1.35
Wolf number	-0.021	0.125	-0.165	0.869	1.01
White-tailed deer density (indiv. 1000 ha-1)	-0.002	0.026	-0.089	0.929	1.36
Variance in territory	1.154				
Residual df	177				
Model 3 (AIC = 243.9, R ² = 0.119)					
Intercept	-1.637	0.841	-1.946	0.052	-
Number of sheep farms in territory	0.075	0.040	2.129	0.033	2.12
Wolf number	-0.051	0.126	-0.404	0.687	1.01
Roe deer density (indiv. 1000 ha ⁻¹)	-0.212	0.162	-1.826	0.068	2.16
Variance in territory	1.014				
Residual df	177				
Model 4 (AIC = 247.2, R ² = 0.039)					
Intercept	-1.885	0.877	-2.149	0.032	-
Number of sheep farms in territory	0.043	0.032	1.336	0.181	1.63
Wolf number	-0.029	0.126	-0.234	0.815	1.02
Total density of ungulates (indiv. 1000 ha⁻¹) Residual df	-0.015 177	0.023	-0.647	0.518	1.65



Fig. 2. Relationships between numbers of sheep farms and population densities of moose, white-tailed deer and roe deer and the numbers of wolf attacks on sheep outside reindeer husbandry area of Finland in 2016–2020.

in which depredation cases were modelled with moose or roe deer density (Table 1). The size of wolf territory did not account significantly for the variation in the number of depredation cases in any of the models (p values ranged between 0.4 and 0.6).

The number of annual cases of wolves killing sheep decreased from ca. 0.5 to 0.1 when moose density increased from 2 to 4 individuals per 1000 ha (Fig. 2).

Discussion

The observed negative relationship between moose density and the number of annual depredation cases in sheep farms suggests that low moose density may increase the risk of wolf attacks on sheep. However, the relationship was not strong and thus it seems that in Finland sheep are not a significant alternative prey for wolves in absence of moose. Furthermore, we found that presence of white-tailed deer did not affect the risk of wolf attacks on sheep, which disagrees with the prey scarcity hypothesis. Both moose and wolves avoid residential areas (Nikula *et al.* 2004, Kaartinen *et al.* 2015), and in Finland the risk of wolf attacks on sheep is also highest in farms in remote locations (Kaartinen *et al.* 2009). The above may partly explain why in our study the number of attacks was related to moose density.

Sheep farms are much less likely to be located far from residential areas, avoided by wolves, in southwestern wolf territories where human and white-tailed deer population densities are higher than in the eastern wolf territories (Kaartinen *et al.* 2009, Kaartinen *et al.* 2015, Kojola *et al.* 2016). In Finland, white-tailed deer prefers mixed forests and agricultural areas (Poutanen 2020) and does not avoid human settlements as much as moose. Roe deer prefer habitats with dense canopy cover (Mysterud *et al.* 1999), but their habitat use in relation to human settlements is not known.

Ungulate density estimates provided by hunters are used for sizing local hunting harvest rates. There may be several hunting areas hosted by different hunting clubs within a wolf territory, thus possible population underestimates and overestimates sufficiently cancel each other out. Although hunters report densities as absolute figures, their main purpose is to provide relative indices for management of ungulate populations. Although formal comparative analysis on different monitoring methods has not been conducted in Finland, it is noteworthy that e.g. moose density estimates correlate with the number of traffic collisions (Niemi *et al.* 2017).

We found no correlation between the numbers of resident wolves and depredation cases. Wild ungulate kill rate per wolf may be negatively related to wolf pack size. In Scandinavia, numbers of moose killed per day per wolf is highest in territories occupied by wolf pairs and lowest in territories occupied by large packs (Zimmermann *et al.* 2014). This pattern weakens the relationship between total number of wolves and the total number of kills in an area. Whether this concerns livestock too, is not known.

Our results do not clearly support either the prey tracking hypothesis or the prey scarcity hypothesis, as the number of annual depredation cases was only related to moose population density. Moose density is regulated by hunting in Finland. The density regulation aims to limit the number of traffic collisions and forest damage caused by moose. Low moose density increases the risk of wolf attacks on hunting dogs (Kojola *et al.* 2022, Kojola *et al.* 2023) and our study suggests that it may also increase the risk of wolf attacks on sheep.

Acknowledgements

We are grateful to field technicians Antti Härkälä, Leo

Korhonen, Reima Ovaskainen, Seppo Ronkainen and Tapio Visuri for collaring wolves and coordinating DNA sampling. Finnish hunting clubs are acknowledged for population density estimates of ungulates.

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