

Research

Does prey scarcity increase the risk of wolf attacks on domestic dogs?

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Gray wolf *Canis lupus* predation on domestic dogs *Canis familiaris* is a considerable wolf–human conflict issue in several regions of Europe and North America but it has not been well documented in the scientific literature. Livestock depredations by wolves may be related to the abundance of wild prey. Regardless of the presumed motivations of wolves for attacking dogs (likely due to interference competition and predation), the abundance of wild prey populations may also influence the risk of wolf attacks on dogs. We examined whether the annual number of fatal attacks by wolves on dogs was related to the abundance of primary prey, including wild boar *Sus scrofa* and roe deer *Capreolus capreolus* in Estonia, as well as the abundance of moose *Alces alces* in Finland. Statistical models resulted in significant negative relationships, thus providing evidence that the risk of attacks in both house yards (Estonia) and hunting situations (Finland) was highest when the density of wild prey was low. Wild ungulates cause damage to agriculture and forestry, but they seem to mitigate conflicts between wolves and humans; therefore, it is necessary to develop a holistic, multispecies management approach in which the importance of wild ungulates for large carnivore conservation is addressed.

Keywords: *Canis lupus*, depredation, domestic dog, grey wolf, human–wildlife conflict, prey scarcity

Introduction

Large carnivores are often key species for ecosystem function and services (Chapron et al. 2014, Ripple et al. 2014). However, the recovery of one of the most controversial apex predators, the gray wolf *Canis lupus* and its ongoing rebounding human-dominated landscapes in Europe and North America has elicited negative reactions (Bisi et al. 2007, 2010, Majic and Bath 2010, Suutarinen and Kojola 2017, Olson et al. 2019, Liberg et al. 2020) although there are also positive reactions (Arbieu et al. 2019). The major wolf–human conflict is represented by livestock depredation that have become

increased when wolf populations have started to expand (Treves et al. 2002, Marucco and McIntire 2010, Marucco and Boitani 2012).

Biological environment may affect the risk of carnivore-caused damages due to potential relationship between the abundance of wild prey population. If any relationships exist, they can be either positive or negative. Prey tracking hypothesis suggests that the presence of wild prey can increase depredation rates by attracting predators and prey scarcity hypothesis, alternatively, assumes that the absence of native prey may facilitate predation on livestock (Nelson et al. 2016).

A locally abundant wild prey may increase the risk of damages because high prey abundance may increase predator's encounters with domestic animals when wild prey and domestic animals overlap spatially (Treves et al. 2004, Bradley and Pletscher 2005, Nelson et al. 2016). Low density of wild ungulates may also be associated with high rates of livestock depredation (Meriggi and Lovari 1996, Meriggi et al. 1996, Sidorovich et al. 2003, Gervasi et al. 2014, Khorozyan et al. 2015) which may support prey scarcity hypothesis.

Interspecific killing is the ultimate outcome of interference competition and is widespread in the carnivore guild (Palomares and Caro 1999). Wolf predation on domestic dogs *Canis familiaris* is a considerable wolf-human conflict issue in several regions of Europe and North America (Fritts and Paul 1989, Kojola and Kuittinen 2002, Kojola et al. 2004, Backeryd 2007, Olson et al. 2015, Peltola and Heikkilä 2015, Tikkinen and Kojola 2020, Bassi et al. 2021). However, it is not well documented in the scientific literature. Wolf attacks on domestic dogs differ conceptually from wolf attacks on sheep and other livestock because they rarely constitute an important part of the diets of wolves (Lescureux and Linnell 2014). Wolves can also occasionally breed with dogs (Hindrikson et al. 2012, Salvatori et al. 2020). The risk of attacks on dogs is fuelling a great displeasure and is likely one of the major obstacles to facilitating wolf recovery in regions where incidences are common (Bisi et al. 2007, 2010, Olson et al. 2015, Peltola and Heikkilä 2015).

The risk of attacks in house yards can be decreased by building a high fence for the dog or by taking the dog indoors in the evening because wolves usually only visit house yards at night (Kojola et al. 2016). However, there are only a few (if any) effective methods for protecting unleashed dogs during hunting. Harnesses with electric deterrents seem to be most promising method (Fedderwitz 2010).

Herein, we examine whether the risk of wolf attacks on dogs is related to the abundance of wild prey. The motivations of wolves to attack dogs can be due to predation for food and territorial defence (Karlsson and Jaxgard 2004). Regardless of the wolves' motivations, the relationship between prey abundance and the number of incidences may be expected. If this is the case, the success of wildlife management in the maintenance of abundant prey populations could mitigate wolf-human conflicts that are due to wolf attacks on dogs. Two previous studies have indicated that the risk of wolf attacks on domestic dogs may be related to the abundance of

wild prey (Kojola and Kuittinen 2002, Werhahn et al. 2019, Bassi et al. 2021), but only Kojola and Kuittinen (2002) have found statistically significant evidence that attacks on dogs were most common in regions where the density of primary prey was low. However, that analysis was based on only four years of data for square areas (2500 km²), and the analysis did not take into account wolf density in the study areas. Herein, we examined spatial and temporal variations in the number of dogs that were killed by wolves by taking into account wolf and prey abundance in two areas (Estonia and eastern Finland).

Study area

We conducted our examination in two study areas (Estonia and eastern Finland) (Fig. 1). Estonia belongs to the south-boreal vegetation zone, and eastern Finland belongs to the mid-boreal vegetation zone (Ahti et al. 1968). For Finland, we limited our study area to six moose management zones that matched the region to which a breeding wolf population occurred throughout our study period (2000–2018; Kojola et al. 2014, 2018). In Finland, the predominance of conifers is higher than in Estonia, where deciduous trees are more common. In our Finnish study area, > 80% of the land is covered by forests (Hansen et al. 2013), which are highly dominated by conifers (Majasalmi and Rautiainen 2021). In Estonia, the proportion of agricultural land is higher, and forest covers remains at 51.4% (Valgepea et al. 2020).

In Estonia, the primary prey of wolves are wild boar *Sus scrofa* and roe deer *Capreolus capreolus* (Valdman et al. 2005). In eastern Finland, moose *Alces alces* constitute 90% of the food biomass consumed by wolves (Gade-Jørgensen and Stagegaard 2000).

Methods

Data

Wolf packs were systematically recorded in both Estonia and Finland (Kojola et al. 2014, 2018, Plumer et al. 2018) with the recordings primarily based on voluntarily provided data. In eastern Finland field technicians of Natural Resources Institute Finland (Luke) conducted snow-tracking and in a remarkable portion of packs (30–60%) at least one wolf was equipped with at least one geographic position system (GPS) transmitter that was fitted on the collar. The capture protocol and permits are described in other studies (Kojola et al. 2006, 2018, Ylitalo et al. 2020). Luke's field technicians also conducted systematic snow tracking to assess approximate territory boundaries for packs without transmitters.

For Estonia, the proxy for the wild boar and roe deer yearly abundance was the number of animals that were harvested. We assumed that hunting harvest was a valid measure of relative abundance because the hunting of these species was not limited by quotas. For our study area in eastern Finland, we used postseason estimates that were provided by each moose

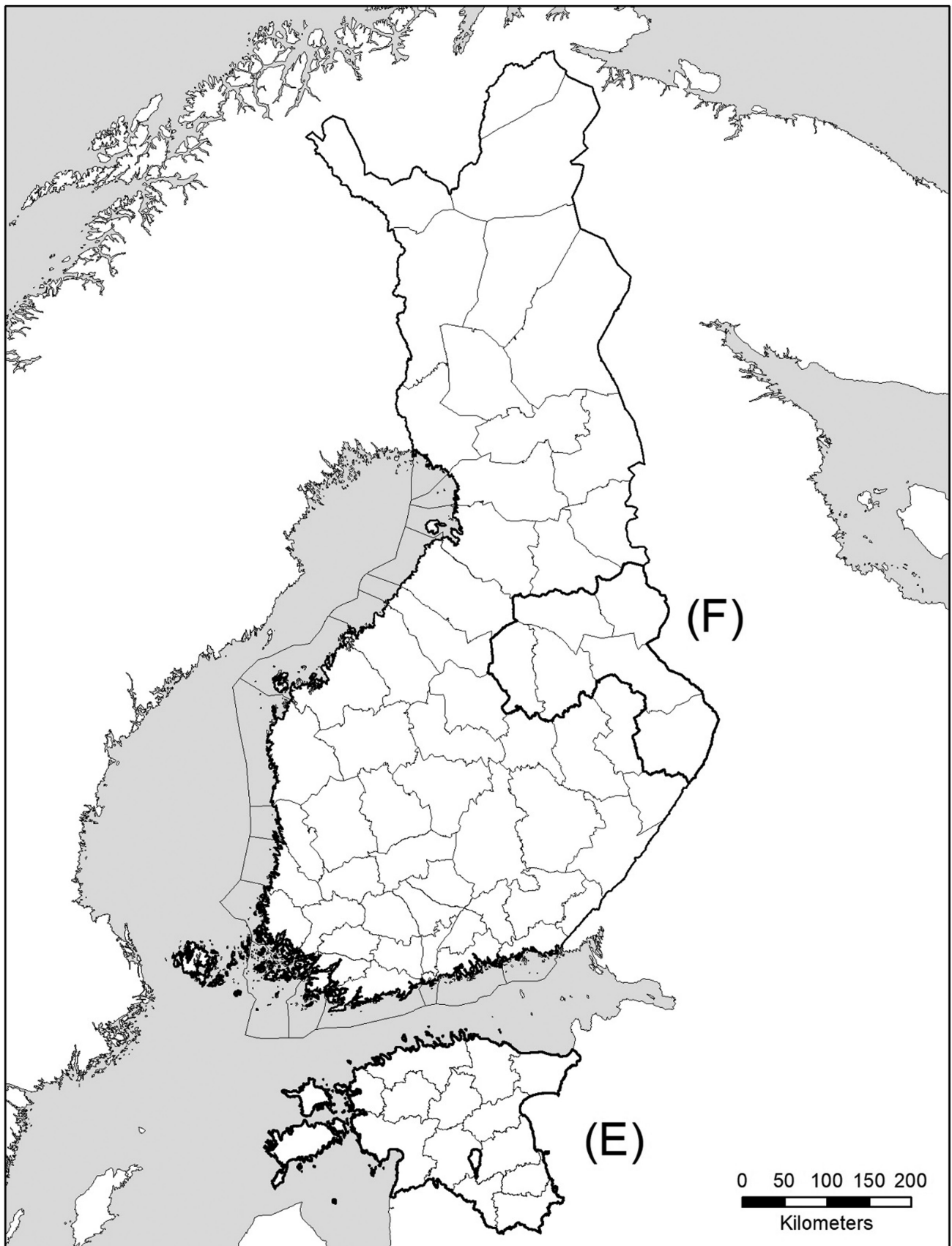


Figure 1. Study areas: Estonia (E) and eastern Finland (F). Map of Estonia show provinces and map of Finland moose management zones.

hunting club for their own hunting area and calculated the preseason moose population by adding the harvest to the postseason estimates. Hunters recorded the number of moose observations per hunting day, which was highly correlated with moose density estimates (I. Kojola et al. unpubl.).

In Estonia the number of dogs killed by wolves was regularly investigated and recorded by state authorities as a part of wolf monitoring since 2002. State compensation scheme was established in 2008. In Finland all dogs killed by wolves were compensated by state since 1996 and the number of dogs that were killed by wolves is the number of dogs that were compensated. Our data was comprised of 168 cases from Estonia and 276 cases from Finland. The records were almost complete because wolf attacks within house yards existed, and only a few hunting incidences remained unsolved because the hunting dogs were regularly collared with transmitters, including GPS components and a global system for mobile devices (GSM) for online mobile phone connections. In Estonia, dogs were primarily killed (> 90%) within house yards, whereas in Finland, wolves primarily killed dogs (> 60%) in hunting situations. Due to the fact that the cumulative number of days when dogs were used in moose hunting was available for each moose management zone in Finland, we accounted for that variable in the statistical analyses for the Finnish data.

Statistical analysis

The count distributions of wolf attacks were skewed and over-dispersed in both countries, especially in the Estonian data. Thus, negative binomial distributions could be assumed in the modelling of the data. The generalized linear mixed models were computed separately for Estonia and Finland. The number of wolf attacks was the response variable in the models. The explanatory variables were the number of moose, the number of wolf packs, the number of dog hunting days and the area where the attacks were counted (moose management areas or parts of the areas) in the Finnish model. The explanatory variables for the Estonia model included the numbers of hunted wild boars or roe deer (both separately), the number of wolf packs and the area where the attacks were counted (area of the regions). The areas were considered as the fixed predictors instead of offset variable, and the estimates were computed at the mean of the areas.

The regions in both countries where the attacks were monitored during the years 2000–2018 in Finland and 2003–2018 in Estonia were treated as random factors in the models. In Finland, there were six moose management zones (MMZs) in eastern Finland and 15 provinces in Estonia (Fig. 1). The annual values were assumed to be correlated in time (AR1). The ACF plots for the response variable (the number of wolf attacks) suggested the existence of an autocorrelation between the current and the previous years. Thus, the AR1 correlation structure was used for the residuals in the models.

Different parametrizations were tested to consider the effect of overdispersion in the negative binomial models.

The negative binomial model was defined by two estimated parameters (mean [μ] and theta [θ] theta was known also as size) (Crawley 2007). The fit to the observed count data (the probabilities of the different counts) could be estimated by AIC and by simulating a curve on the observed count probabilities by using the two parameters in the simulations.

In the negative binomial distribution, the variance could be expressed as $\mu + \mu^2/\theta$, where θ (theta) denotes the clumping parameter. This parametrization is called NB2 (Fournier et al. 2012, Skaug et al. 2014). Another parametrization is called direct parametrization, which directly estimates the dispersion. The direct parametrization is also called NB1 (Fournier et al. 2012, Skaug et al. 2014).

The parametrizations of dispersion could affect the results (Crotteau et al. 2014). These two parametrizations were tested for Finnish and Estonian data by using the R package *glmmADMB* and its function *glmmadmb* (Fournier et al. 2012, Skaug et al. 2014). The NB1 parametrization produced a lower AIC in the Finnish model (451.1 versus 460.0) and was used in the final *glmmPQL* model; however, the NB2 parametrization gave a better fit in the Estonian model (AIC: 398.9 versus 407.4) and was used in that model as theta.

The final negative binomial mixed model with AR1 structure was computed by using the R package *MASS* with the use of its function *glmmPQL* (Venables and Ripley 2002). The predictions for the models were computed by using the R package *effects* (Fox 2003, Fox and Weisberg 2019). The predictions were transformed back to the original scale by using an exponent of the predictions and a ratio estimator in the correction of the estimates (Snowdon 2011). The trigamma coefficients of determination were computed by using the R package *MuMIn* (Barton 2020).

Results

In Estonia, the abundance of the primary prey of wolves significantly varied during the study period (Fig. 2). Hunting bags for both roe deer and wild boar increased in the first years, but the roe deer harvest started to decrease earlier than the wild boar harvest, which peaked in 2015 before a rapid decline (Fig. 2). The roe deer harvest increased from 2012 and onwards (Fig. 2). In contrast, moose abundance in eastern Finland showed a gradual decreasing trend over the study years (Fig. 2). The mean number of dogs that were killed annually by wolves per unit area was a parameter that varied most between the study areas (Fig. 3). The mean number of packs increased in Estonia from 2003 through 2007 but did not show a pronounced trend during 2008–2018 (Fig. 3). In Finland, the mean number of packs had two peak years (in 2005 and 2015) (Fig. 3).

The model for Estonia provided evidence that fatal attacks on dogs were decreased in years when roe deer and wild boar were more abundant (Table 1, Fig. 4). In the model for eastern Finland, the number of dogs killed per year was also negatively influenced by the abundance of primary prey (moose, Table 1, Fig. 5). The number of wolf-killed dogs was

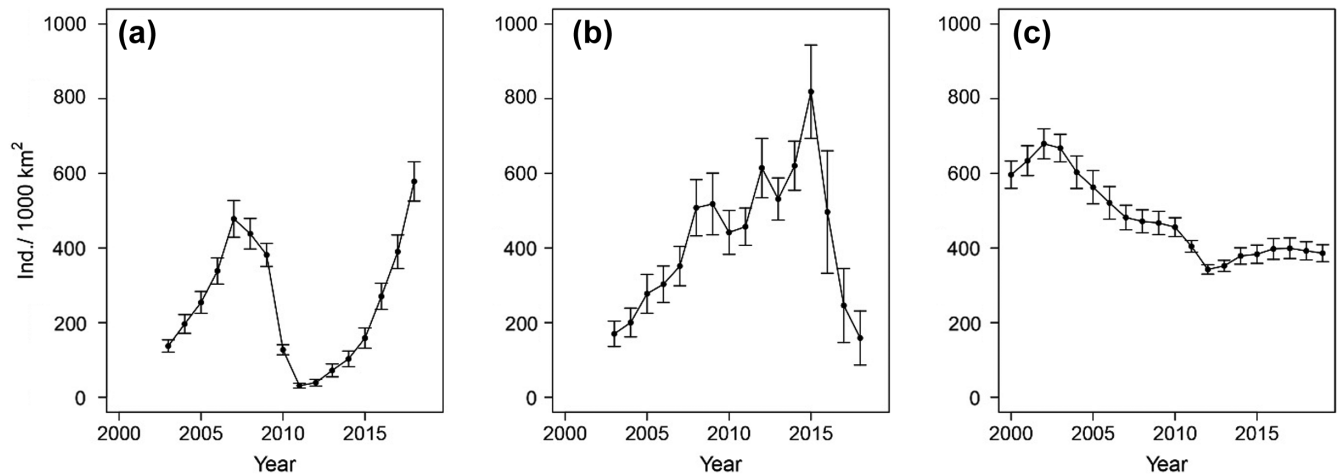


Figure 2. Mean (\pm SE) roe deer (a) and wild boar (b) harvests in Estonian provinces and moose density (c) in moose management zones in eastern Finland, 2003–2018.

related to the number of wolf packs ($p=0.046$) and the area of the province ($p=0.025$) in Estonia but not to the number of packs or the area of moose management zone in Finland (Table 1).

The observed versus simulated probabilities of the counts (Fig. 6) suggested that the models for Estonia and Finland fitted to the data reasonably well. However, the Estonian model slightly underestimated (about 10%) the zero observations

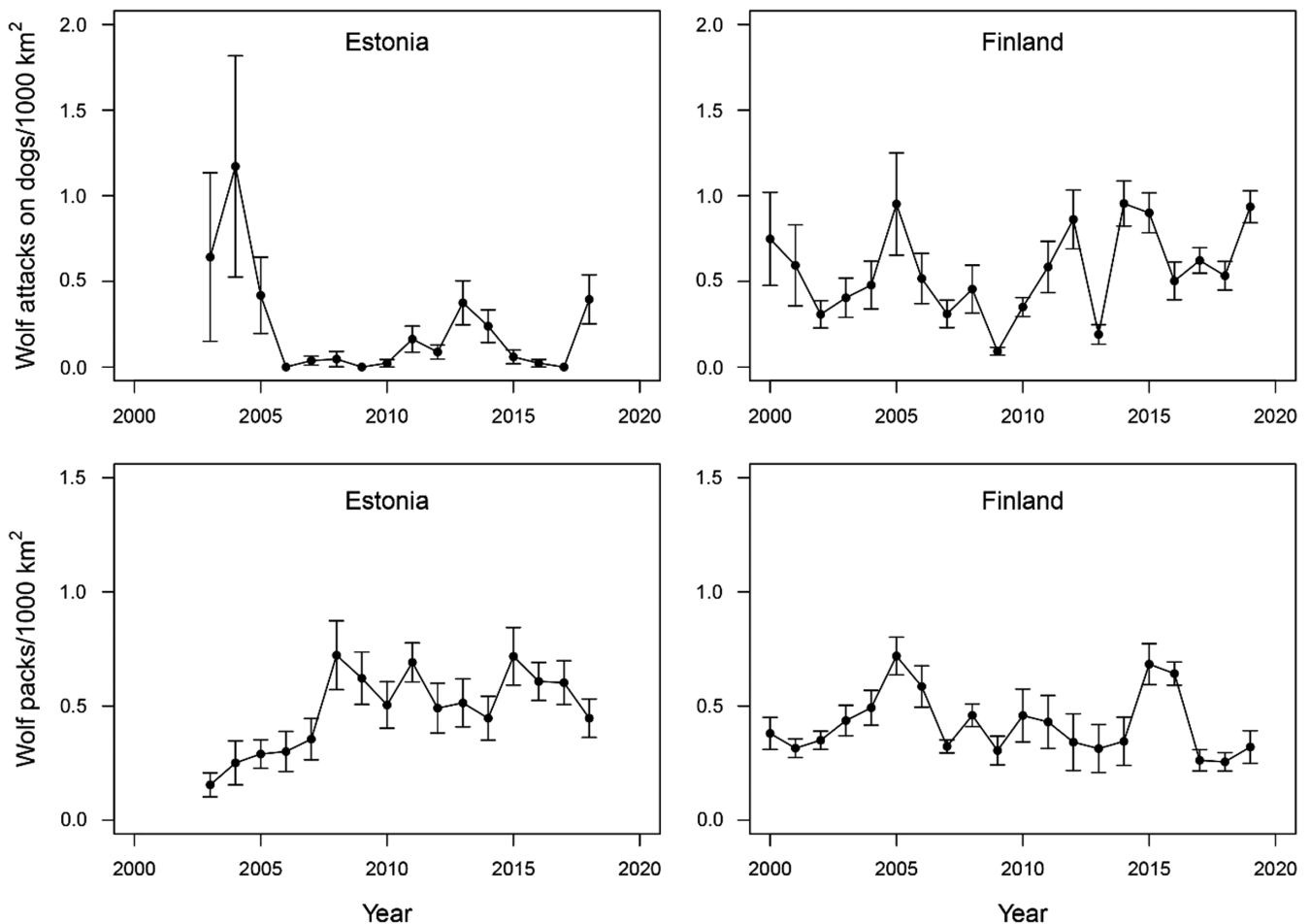


Figure 3. Mean (\pm SE) number of dogs killed by wolves and mean number of wolf packs in Estonian provinces and moose management zones in eastern Finland per 1000 km², 2003–2018.

Table 1. Parameter estimates and tests for the generalized (negative binomial) mixed models for dogs that are killed yearly in Estonia and eastern Finland.

Variable	Estimate	SD	df	Student's t	p
Model 2. Estonia, R ² (trigamma): marginal 20.9%, conditional 23.6%					
Fixed effects					
Intercept	−1.042	0.751	222	−1.389	0.166
Province, km ²	5.456 e ^{−4}	2.467 e ^{−4}	13	2.212	0.046
Wolf packs (n)	0.353	0.156	222	2.262	0.025
Roe deer harvest (ind.)	9.243 e ^{−4}	3.677 e ^{−4}	222	−2.514	0.013
Wild boar harvest (ind.)	1.413 e ^{−3}	0.357 e ^{−3}	222	−4.108	< 0.001
Random effects, phi, theta					
Province (random intercept)	0.215				
Theta	0.329				
Phi (AR1)	0.214				
Model 1. Finland, R ² (trigamma): marginal 50.6%, conditional 55.7%					
Fixed effects					
Intercept	−2.182	1.840	105	−1.186	0.238
Moose management zone, km ²	8.932 e ^{−4}	3.311 e ^{−4}	4	2.698	0.052
Wolf packs (n)	0.122	0.079	105	1.552	0.124
Moose (ind.)	7.285 e ^{−4}	2.847 e ^{−4}	105	−2.559	0.012
Hunting days with dogs (n)	0.604 e ^{−4}	1.015 e ^{−4}	105	−0.315	0.753
Random effects, phi, theta					
Moose management zone	0.092				
Theta	0.369				
Phi (AR 1)	0.294				

and the model for Finland overestimated the zeroes (about 13%). The very skewed observed distribution in the Estonian data also caused underestimated simulated values for the biggest observed counts. The feature could also be seen in the Finnish data (Fig. 6). The predicted mean values corresponded rather well to the observed ones, in the Estonian models being 0.70 (observed) and 0.62 (predicted) killed dogs and in the Finnish model 2.86 (observed) and 2.95 (predicted) killed dogs.

Discussion

The negative relationship between ungulate abundances and the number of domestic dogs killed by wolves were in accordance with the prey scarcity hypothesis that was, however, formulated to concern the risk of livestock depredations by large carnivores (Nelson et al. 2016). Motivation to kill a sheep is predation while a motivation to kill a dog may be elimination of a potential competitor. Interspecific killing is a widespread outcome of interference competition in carnivore guilds (Palomares and Caro 1999), it may explain the wolves' attacks on domestic dogs in many cases; however, dogs may also be an alternative prey for wolves more often when the abundance of wild prey is low. Usually, the wolves partially or fully eat the dog they have killed, with the proportion of eaten kills ranging between 72 and 96% (Fritts and Paul 1989, Kojola and Kuittinen 2002, Backeryd 2007, Bassi et al. 2021). Although wolves usually consume the dogs that they have killed, dogs have only a marginal role as wolves' prey (Lescureux and Linnell 2014). In Estonia the majority of wolves that killed dogs are identified to be sub-adult vagrants or pairs moving often near residential areas

(M. Kübarsepp and P. Männil unpubl.). Such wolves are seeking for or just going to establish their own breeding territory and may be motivated to remove potential competitors. However, it is obvious that wolves can catch dogs more readily than wild prey, and subadults that are still unexperienced as hunters may face difficulties more often than adult wolves. Dispersing individuals may at least consume more livestock than stable packs (Imbert et al. 2016). Documented cases of the behaviours of wolves and dogs in wolf–dog encounters are too few for a formal analysis, which could result in a better understanding of the wolves' motivations. During the hunt, the situation wherein a moose hunting dog is barking at a moose that is far from the hunter could be a likely situation where the wolf is motivated by competition for the shared 'prey'. The breeds that are most frequently used in moose hunting in Finland are Norwegian and Swedish moose dogs, which are relatively tall dogs weighing between 15 and 30 kg. Many hounds are attacked by wolves and, in most cases, when they are hunting mountain hares *Lepus timidus* (Kojola and Kuittinen 2002) that are also the prey of wolves (Gade-Jørgensen and Stagegaard 2000). Wolves in Finland occasionally kill red foxes, and their primary prey is the mountain hare (Kojola et al. 2017). The attacks on dogs are focused near territory boundaries, which may indicate that one reason for the attacks may be due to territorial defence (Tikkunen and Kojola 2019).

Our results provided evidence that in Estonia, where the primary prey of wolves (wild boar and roe deer) are smaller and, therefore, easier to catch than moose, the risk of attacks on dogs was high only in a few selected years when their densities were remarkably lower, compared to their ordinary abundances. In Scandinavia, the proportion of roe deer is higher in kills by wolf pairs than packs (Sand et al. 2016),

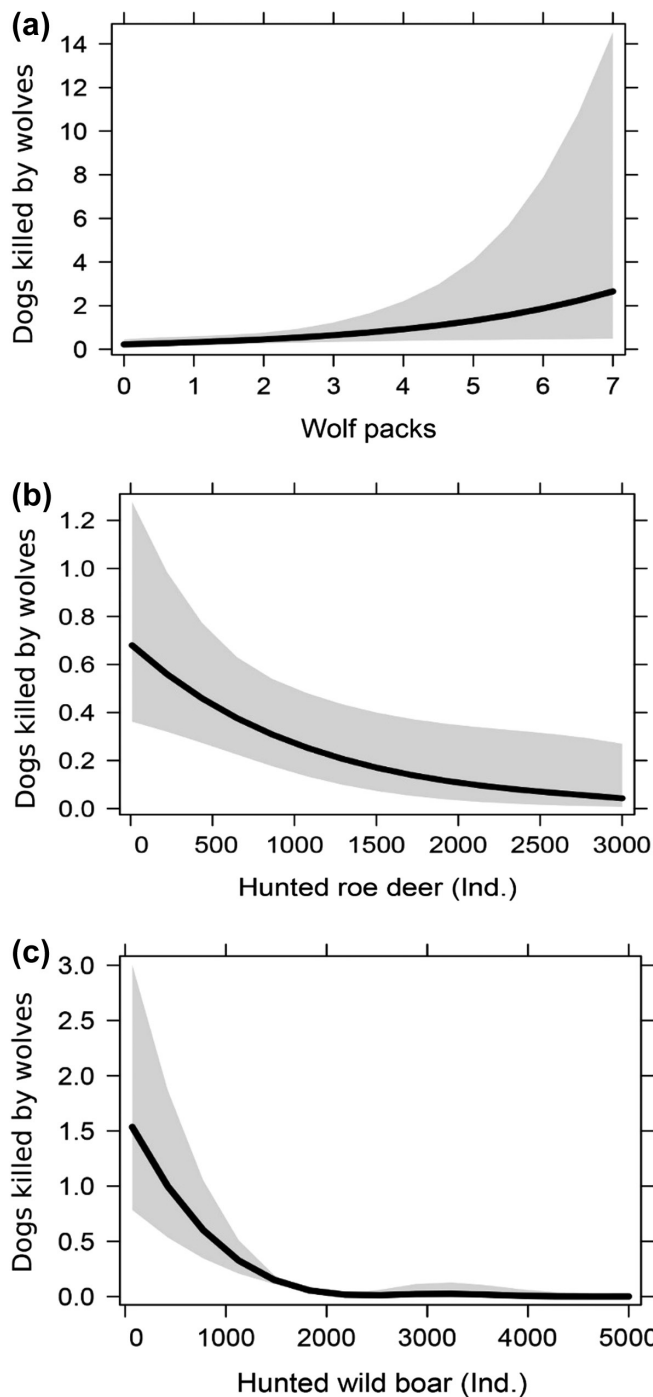


Figure 4. Relationships of the number of wolf packs (a), roe deer (b) and wild boar (c) that were harvested to the number of dogs that were killed annually by wolves in Estonia (cf. Table 1), 2003–2018. Grey zones are 95% confidence intervals.

and wolf territory size is negatively related to the abundance of roe deer but is not negatively related to the abundance of moose (Mattison et al. 2013). These findings indicate that both the density of primary prey and the presence of alternative, easier-to-catch prey may have an impact on the risk of wolf attacks on dogs. Data from Finland provide evidence

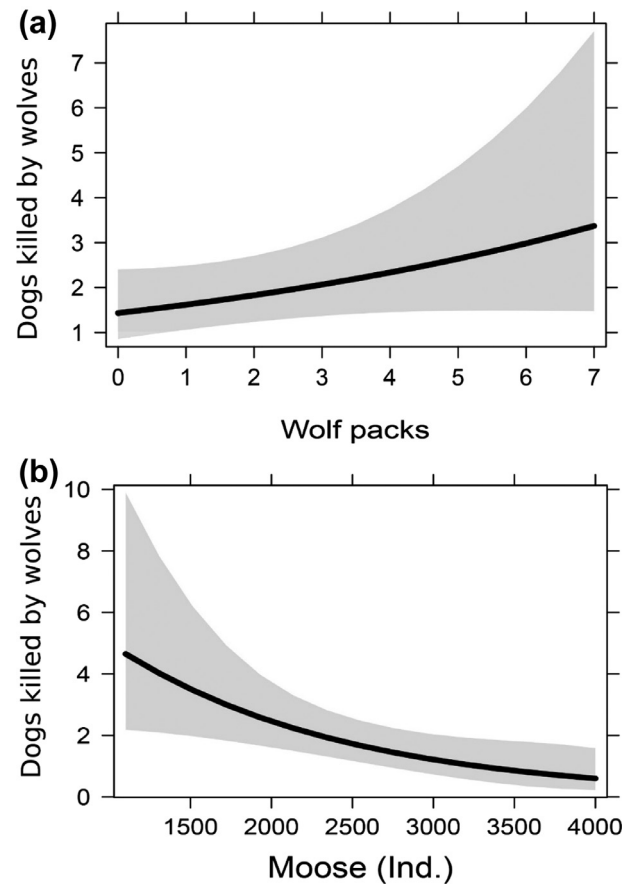


Figure 5. Relationship of the number of wolf packs (a) and moose abundance (b) to the number of dogs that were killed by wolves in Finland (cf. Table 1), 2000–2018. Grey zones are 95% confidence intervals.

that considerably fewer hunting dogs are lost to wolves in southwestern Finland, where white-tailed deer *Odocoileus virginianus* and moose share the wolf as a common predator (I. Kojola et al. unpubl.).

In eastern Finland, where most dogs are lost to wolves during hunting, moose density was observed to gradually decrease during the study. However, the number of dogs lost to wolves showed a large between-year fluctuation that was due to reasons that we could not determine in this study. The differences in the number of attacks may be high even between neighbouring territories (Kojola et al. 2004).

The differences between the study areas are noteworthy. The indication that the number of dogs killed by wolves was related to the number of wolf packs only in Estonia could be due to the fact that cases in Finnish study area are mostly connected to hunting with dogs, and hunters might be more reluctant to release their dogs in years when signs of wolf presence were most common. Owing to higher human density in Estonia than Finland (means 29 and 14 people km⁻²) wolves may move closer to human settlements which might be a concurrent cause of attacks on dogs. On the other hand, the risk of attacks in Finland is smallest in wolf territories located in the southwestern part of the country where human

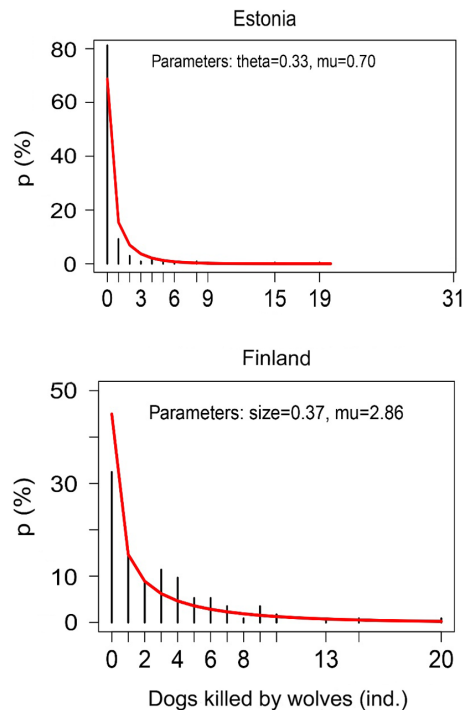


Figure 6. Model fits to data. Comparisons of the probabilities of observed and simulated counts. The simulations are made using the negative binomial parameters μ and θ .

densities are remarkably higher than in our study area in eastern Finland (Kojola unpubl.). The reason for the area (province in Estonia, moose management zone in Finland) being significant only in Estonia might be owing to higher differences in the areas of Estonian provinces (Fig. 1).

Prey populations in Estonia and Finland are limited by several factors, including predation by carnivores and harvest by humans. In Estonia, the crash of the wild boar population during 2015–2018 was caused by the outbreak of African swine fever (Nurmoja et al. 2017, Schulz et al. 2020). These types of disease outbreaks are unpredictable; therefore, they are practically impossible to prevent by means of management interventions. Diseases are seldom the primary reason for population fluctuations of the primary prey of wolves; therefore, we focused on discussing management policies that would decrease the risk of wolf attacks on dogs in more ordinary situations.

Management implications

Abundance of wild ungulates are regulated by means of hunting in many places in Europe. The motivations of management authorities in limiting densities are often reasoned by economic loss due to browsing and grazing by herbivorous animals and human safety due to traffic accidents (Apollonio et al. 2017, Valente et al. 2020). Ungulates are ecosystem engineers and an integral part of both ecosystems and ecosystem management (Smit and Putman 2011, Apollonio et al. 2017). Our results did not call for high, costly ungulate densities to mitigate wolf–human conflict but

provided a signal that low densities may increase the risk of attacks on domestic dogs.

A multispecies approach aimed at managing large-scale carnivore and ungulate populations that also accounts for species interactions in variable environments would be a useful element of management strategies. Another necessary step aimed at maintaining viable large carnivore populations (without the risk of escalation of damages caused by carnivores to livestock, the loss of domestic dogs to wolves and damage caused by ungulates to forestry and agriculture) may be the continuous evaluation of management interventions and readiness to flexibly modify management policies whenever the situation is necessary. Anyhow, a better protection of dogs should also be established.

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Author contributions

Ilpo Kojola: Conceptualization (lead); Writing – original draft (lead). **Ville Hallikainen:** Formal analysis (lead). **Marko Kübarsepp:** Data curation (equal); Investigation (equal). **Peep Männil:** Conceptualization (supporting); Data curation (equal); Investigation (equal); Writing – review and editing (equal). **Mari Tikkunen:** Conceptualization (equal); Data curation (equal); Writing – review and editing (equal). **Samuli Heikkinen:** Project administration (equal); Validation (supporting); Visualization (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <<https://datadryad.org/stash/dataset/doi:10.5061/dryad.xd2547dk2>> (Kojola et al. 2022).

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