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RESEARCH

Artificial nest predation, relative abundance, and activity patterns of mesocarnivores in relation to wild boar presence

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Abstract

Intensifying nest predation is one of the suggested factors causing the wide decline of ground-nesting birds. Predation rates often increase with growing predator numbers, especially of invasive species. The emerging effects of novel species may, however, be hard to quantify due to interactions with native species. The wild boar (*Sus scrofa*) has recently expanded its range into Finland through natural dispersion, marking a significant northward extension of the range. In this ecosystem, little is known about the direct and indirect roles of wild boars as nest predators. Especially the potential avoidance of wild boars by other mammalian nest predators has not been studied. To address this gap, we conducted artificial nest and scent post experiments with camera traps on sites of wild boar presence and absence. We found that predation rates by wild boars were at similar modest levels than the rates of other mammalian predators in the area. No significant differences in the overall likelihood of nest predation or nest visits by mesocarnivores were observed between the study areas. Based on the scent post indices, however, mesocarnivores were less abundant on wild boar sites. Our study concludes that the effects of wild boars on nest survival rates are small at their current low densities. The study also provides a baseline for monitoring, as wild boars are expected to expand their range and density in the future.

Keywords Camera trap · Scent post · Raccoon dog · Supplemental feeding · Nest loss

Introduction

Many boreal ground-nesting bird populations have experienced long-term declines in the past decades, including waterfowl, wader, and forest grouse species (Lehikoinen et al. 2016; McMahon et al. 2020, 2024; Pöysä et al. 2023; Reif et al. 2023). While the declines may result from several biotic and abiotic factors affecting various facets of the birds' life history, nesting failures are, to a major extent, caused by predation (Klett et al. 1988; Newton 1998; Macdonald and Bolton 2008Holopainen et al. 2015, 2024a; Palencia and Barroso 2024). Nest predation risk, in turn, is most affected by the abundance and species composition of predators, which include a variety of mammals, birds and reptiles. The local abundances and diet preferences of predator species can directly affect nest predation rates (Kurki et al. 1997; Kauhala 2004; Dell'Arte et al. 2007; Nummi et al. 2019; McMahon et al. 2024). However, predation risk may also be affected indirectly e.g., through predator–predator interactions. These intraguild effects may be spatial or temporal (or both) and include exploitation competition or interference competition such as avoiding larger predators due to the risk of being eaten or attacked (Holt and Polis 1997; Fedriani et al. 2000; Selonen et al. 2022; Allen et al. 2024). Mesopredators are often focal species in nest predation research, as they pose great risks not only to eggs but also to fledglings

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and incubating females (Ackerman et al. 2003; Macdonald and Bolton 2008; Holopainen et al. 2020).

In Finland, pine martens (*Martes martes*), badgers (*Meles meles*), and red foxes (*Vulpes vulpes)* are the most common native mammalian nest predators according to artificial nest experiments (Krüger et al. 2018; Holopainen et al. 2024b). Introduced alien species have also entered the guild during the past century. Since the 1930 s, raccoon dogs (*Nyctereutes procyonoides*) have spread across southern and central Finland, where their nest predation rates exceed those of native predators (Krüger et al. 2018; Holopainen et al. 2021). This is likely due to raccoon dogs having become the most abundant mesopredator species in given areas (Selonen et al. 2024). Introduced American mink (*Neovison vison*) is also shown to have substantial negative effects on bird breeding success (Nordström et al. 2002; Bonesi and Palazon 2007; Brzeziński et al. 2012, 2020). However, minks are highly adapted to aquatic habitats, which limits their presence in more terrestrial ecosystems, unlike raccoon dogs that can thrive in a variety of environments, including forests and fields (Schooley et al. 2011; Holopainen et al. 2021).

In addition to introduced aliens, novel species have also settled in Finland via natural northward dispersion. After ca. 8000 years of absence, the first wild boars (*Sus scrofa*) arrived in Finland in the 1950s. Since then, the population has increased most notably within the past two decades (Erkinaro 1982; Ukkonen et al. 2015; Kukko et al. 2018). The current population (ca. 2000 individuals) is heavily weighted in the southeastern border region, with maximum densities of 30 to 50 individuals per 100 km^2 (Ruha and Kunnasranta 2024). So far, their local role as predators has not been studied. Elsewhere in Europe, with much denser wild boar populations, the species has been shown to be a major nest predator of ground-nesting birds (Saniga 2002; Purger and Mészáros 2006; Svobodová et al. 2012; Carpio et al. 2014, 2016; Senserini and Santilli 2016; Oja et al. 2017; Mori et al. 2021). However, wild boars have also been suggested to affect mesocarnivore presence both spatially and spatiotemporally: Carpio et al. (2016) suggested that, in Sweden, wild boars may benefit local wader nesting by repelling mesocarnivores, while Osugi et al. (2019) observed that raccoon dogs avoided cherry fields during times of high wild boar activity. The potential direct (i.e. negative) and indirect (i.e. positive) effects of wild boars on ground-nesting birds are likely dependent on wild boar density and the species composition of the local predator community.

To examine the direct and indirect roles of wild boar on ground nest predation, we monitored the survival of artificial nests along with mesocarnivore visits at nests and scent posts within and outside of the current settled wild boar distribution in southern Finland. Our aims were (1) to assess the portion of nest predation by wild boars and (2) to study whether wild boar presence affects mesopredator nest predation, relative abundance, and activity. Based on earlier evidence (Carpio et al. 2016; Osugi et al. 2019) from Sweden and Japan, we hypothesize that (1) wild boars depredate ground nests, (2) nest predation rates by and the relative abundance of mesocarnivores will be lower on wild boar sites, and (3) the diel activity patterns of mesocarnivores will be negatively related to wild boar activity.

Materials and methods

Study area

The study was conducted on 54 sites, located across southern Finland, between 2015 and 2021. Six of the 54 sites had only scent posts, while the rest of them had the complete set up. The sites were mosaics of forests and agriculture, with patches at least 300 m in width in both landscapes to account for potential edge effects. Twenty-three sites were located within the established wild boar distribution area in southeastern Finland (Fig. 1). To verify wild boar presence, sites where only accepted for this research if the landowners or hunters reported wild boars visiting the nearby feeding sites within two weeks prior to the start of the experiment.

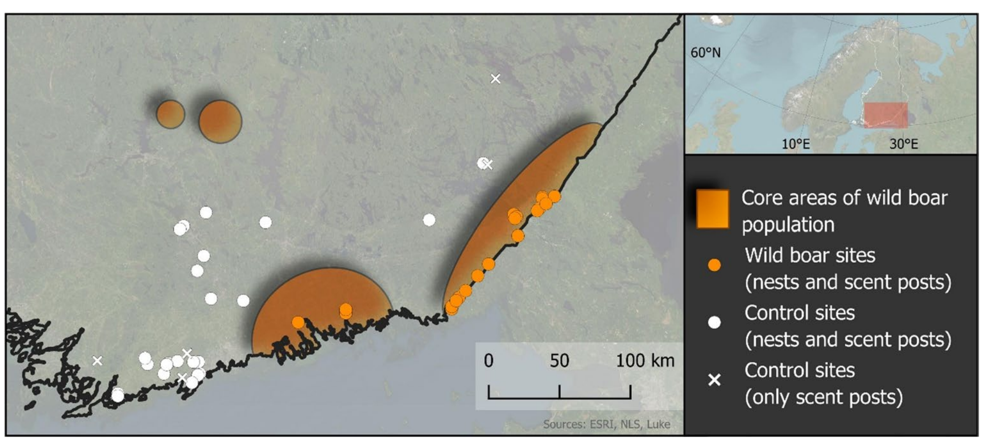

Fig. 1 The study sites in wild boar (N=23) and control areas (N=31). The approximate core areas of the Finnish wild boar population (over 10 individuals/100 km^2) are based on population estimates by Ruha and Kunnasranta (2024)

Control sites (N=31) were located outside of the established wild boar range (Fig. 1), although vagrant wild boars may occur throughout southern Finland, including the control areas. While the study areas have broadly similar climates and vegetation (mainly coniferous forests), there is a slight cline between the hemiboreal southwest and boreal east. Similarly, mosaics of agricultural lands and deciduous forests are more prominent in the southwestern regions and coniferous forest cover increases eastwards (Kersalo and Pirinen 2009). According to the elevation model by National Land Survey of Finland (2025), the study area is lowland with both control sites and wild boar sites varying between 10 and 120 m from sea level. Ground-nesting bird assemblages are similar throughout the study area, but their abundances may vary locally (Valkama et al. 2011): Typical ground-nesting bird species in the forests and fields include hazel grouse (*Tetrastes bonasia*), black grouse (*Lyrurus tetrix*), capercaillie (*Tetrao urogallus*), Eurasian woodcock (*Scolopax rusticola*), northern lapwing (*Vanellus vanellus*), common curlew (*Numenius arquata*), mallard (*Anas platyrhynchos*), common teal (*Anas crecca*) and wigeon (*Mareca penelope*), in addition to many small passerines. Apex predators occur in the study area, with wolf (*Canis lupus*) and Eurasian lynx (*Lynx lynx*) observed all around southern Finland, and brown bears (*Ursus arctos*) more abundant near the easternmost control and wild boar sites (Luke 2025). In the established wild boar areas, supplemental feeding for bait hunting is active year-round. Elsewhere the feeding is targeted at cervids and typically restricted to autumn and winter (i.e., not available during the bird breeding season).

Artificial nests

During the breeding season of forest grouses (late April–June), six artificial nests were placed on each of the 48 nest experiment sites (23 wild boar sites and 25 control sites). Following the protocol by Krüger et al. (2018), two nests were placed in each of the three zones formed based on their distance to the nearest forest edge (50–150 m within a forest, 0–50 m within a forest and field, and 50–150 m in a field). The final distance metres within the zone limits were chosen with a random number generator application. Forest nests were placed so that they were sheltered by a tree, bush, or other vegetation on one side. Field nests were placed in ditches, field margins, or small bush or forest patches to avoid both trampling the crops and damage to nests (and cameras) by farming machinery. Within each site, the average distance between artificial nests was 578 m (range: 33–2849 m). Experimental nest density was designed to be low, to increase observation independence and to avoid density-dependent nest predation (Gunnarsson and Elmberg 2008).

Artificial nests were made by pressing a shallow dent in the ground and covering the bottom of the dent with any soft materials (e.g., hay) within reach around the nest. Four eggs of farmed pheasant (*Phasianus colchicus*) were placed in the nest. Eggs and nest materials were handled with gloves to minimize human scents. A motion-triggered camera trap (Uovision UM565, Uovision UM785, Niteforce 2G-SMS, Akaso 12MP, or Burrel S12 HD) was set at least 1.5 m from the nest, so that the eggs are visible in the images. In forests, all camera traps were attached to nearby trees (or equivalent), while some field nests required installing 1.5-m tall wooden poles for the camera trap. The motion-triggered cameras were programmed for 24-h operation with a delay of 10 s after three successive images. Nests were set in the daytime (9:00–16:00), and each nest experiment lasted for eight consecutive days with no researcher visits during the experiment. The eight-day experiment mimics the early stage of egg laying, when the hen is not yet incubating and thus is absent from the nest.

In addition to predation, visits by mammal predators were counted from camera trap images. An individual was considered new if the previous individual of the same species had been absent for 30 min or more (based on Croston et al. 2018; see Holopainen et al. 2021). Visits were analysed as the total amount during the eight-day trial period, but also separately for the periods before and after predation.

Scent posts

Following the artificial nest experiment on each site, four of the nests were randomly selected (so that all distance zones were represented) and replaced with scent posts to assess the relative abundance of predators in the study sites. The selection was random within each distance zone. In addition to all nest experiment sites, scent posts were set to six additional sites (Fig. 1). Scent posts were made by dipping the tip of a 10–20-cm long twig in gray fox (*Urocyon cinereoargenteus*) gland lure (Gray Ambush by J.R. and Sons) and placing the non-scented end into the ground. Some of the scent was also smeared onto a nearby stone to avoid animals carrying the scent away. Camera traps were positioned 2–3 m from each scent post and left undisturbed for five days. Individuals visiting scent posts were separated with the same 30-minute threshold as those visiting nests.

Analysis

The proportion of agricultural lands surrounding each nest was calculated for 50-, 200-, and 1000-metre radii from Corine Land Cover data (20-m resolution, Finnish Environment Institute) using QGIS (v.3.30.1; QGIS Development Team 2023). As the sites were in forest–field mosaics, the two habitats have a strong negative correlation with each other, enabling a sufficient landscape characterization with just the proportion of agricultural land. The implemented buffer radii are commonly used in landscape effect research (Saab 1999; Laidlaw et al. 2015; Ellis et al. 2020). In addition, a landscape radius of 3000 m around the geometric centre point of all nests within a site was used for relative predator abundance assessment. This radius was selected to ensure all nests (and their surroundings) fall within this landscape buffer. While other landscape features (e.g., waters and infrastructures) may also affect predator–prey interactions, they were omitted, as their proportions and sample distributions were insufficient for reliable analysis. On wild boar sites, the distance to the nearest active supplemental feeding site was measured.

A nest was considered predated if at least one of the eggs was broken or missing at the end of the experiment. As this study focuses on mammal predation and relative abundance, avian predation is included descriptively but not included in any further analyses. To study mesocarnivore predation specifically, we used the generalized linear mixed model (GLMM) framework to calculate daily nest predation probability using modified logistic regression, which incorporates the number of exposure days (eight, each beginning at 12:00) into the link function (Shaffer 2004). This logistic exposure method is a modification of logistic regression and maximizes the use of nest predation data by treating each measurement day as a discrete trial. Daily nest fate was analysed as a binary response variable (0 = survived, 1 = predated). The remaining days were omitted from the data along with predation days of other than mesocarnivore predation. GLMM was also used when analysing nest visits (Zero-inflated poisson) and scent post visits (Zero-inflated negative binomial).

The variables included as fixed effects in analyses were Area (wild boar/control), Day of exposure, Year, Distance to edge, Habitat (forest/field), and Proportion of agriculture (in the radii of 50 m, 200 m, and 1000 m). Site was used as a random effect. The simplest models were achieved in model selection by backward stepwise selection until the Akaike information criteria (AIC) value was minimised. As the scent posts were used to describe relative predator abundance site-specifically (not for each nest), the counts on each site were pooled and analysed with an offset variable (camera-days). When analysing the effect of supplemental feeding, only wild boar sites were included in the models, as feeding was absent in control sites. To analyse the temporal activity patterns of predators, all mesocarnivore observations (with visiting time rounded to the nearest hour) from nests and scent posts were pooled.

R software (R Core Team 2021), glmmTMB package (Brooks et al. 2017), and the protocols by Zuur et al. (2010, 2016) were used to perform the predation and visit analyses. Activity analyses were conducted using the density comparison of the sm package (Bowman and Azzalini 2024).

Results

Nest predation

The artificial nests ($N = 134$) on wild boar sites had a predation rate of 46%, while 32% of the control site nests ($N = 145$) were predated. Wild boars predated only 3% of the predated nests on the wild boar sites. On the control sites, wild boars were not observed in nest or scent post camera traps. Mesocarnivores accounted for 15% of predation events on wild boar sites and 38% on control sites (Table S2). Among these, the raccoon dog was the most common predator (3% on wild boar sites, 21% on control sites) followed by badger (5%, 13%), pine marten (3%, 4%), and red fox (3%, 0%, respectively). Also white-tailed deer (*Odocoileus virginianus*) trampled one nest on a control site. Avian predation was more prominent on wild boar sites (75% compared to 47% on control sites), with most predations by the hooded crow (*Corvus corone cornix*; 31%, 32%) and magpie (*Pica pica*; 16%, 11%, respectively). In ten cases, the predator was not identified due to poor image quality or camera trap failure. The daily risk of mesocarnivore predation on wild boar sites was 3.8% (95% C.I. 0.5–21.8%) and 4.3% (0.7–23.5%) on control sites, with no significant difference between the two ($Z = -0.60$, $P = 0.55$; Fig. 2a, Table S1a).

Nest visits

In addition to realized predation, the number of visits ($N = 156$) at nests were also analysed to further illuminate potential predation pressure. Within their distribution area, wild boars visited artificial nests 0.13 times on average during the study period. The most common visitor was the raccoon dog (0.24 on wild boar sites and 0.39 on control sites) followed by the red fox (0.10, 0.09), badger (0.07, 0.13), and pine marten (0.03, 0.06, respectively). On average, 0.28 mesocarnivores visited each nest in the wild boar area and 0.31 in the control area, with no significant difference ($Z = -0.46$, $P = 0.65$; Fig. 2b, Table S1b). Of all nest visits, 31% occurred before predation, i.e. the animal passed the nest without predating eggs (potentially fearing of the camera trap or in a non-foraging internal state). No differences between areas were found when analysing visits before and after predation separately. Similarly, no species-specific differences among predators were found regarding predation or the frequency of nest visits.

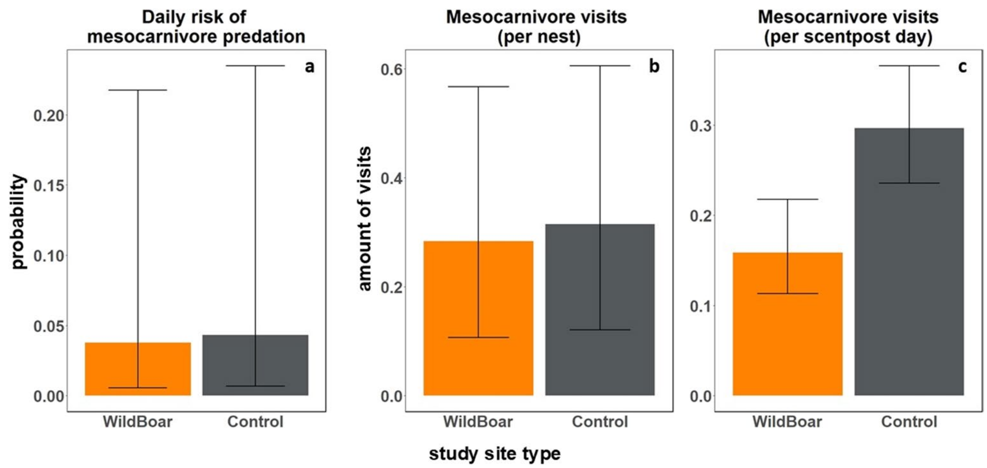

Fig. 2 Nest predation risk (**a**), nest visits (**b**), and scent post visits (**c**) by mesocarnivores on sites of wild boar presence and absence with 95% confidence intervals

Scent post visits

During the 1045 scent post days, 327 mesocarnivore visits were recorded. Based on the results, mesocarnivores were less abundant on the wild boar sites (0.15 observations per scent post day) compared to the control sites (0.29; Z=−5.41, $P<0.005$; Fig. 2c, Table S1c). The same pattern was found species-specifically for raccoon dogs and badgers, but no significant differences were observed with red foxes and pine martens. Raccoon dogs were recorded 0.09 times per camera per scent post day on wild boar sites and 0.20 on control sites (Z=−2.69, $P=0.007$). With badgers, the index was 0.03 on wild boar sites and 0.09 on control sites (Z=−2.15, $P<0.032$).

Activity patterns

The combined data of all recorded camera trap visits (Fig. 3, Fig S1) show the predominantly crepuscular and nocturnal activity of mammalian predators (as well as the diurnal activity of corvids; Fig S1). We observed no significant differences in activity patterns between wild boar sites and control sites for raccoon dogs ($P=0.77$), red foxes ($P=0.92$), badgers ($P=0.28$), or pine martens ($P=0.42$).

Effects of landscape and supplemental feeding

The proportion of agricultural land within 200 m of a nest increased the daily probability of predation (Z=2.27, $P=0.02$; Table S1a) and visits (Z=2.44, $P=0.01$; Table S1b) by mesopredators. The radius of 200 m yielded the highest correlations when compared to the landscapes within 50 m and 1000 m. Mesocarnivore visits were more likely in forests (when compared to fields; Z=2.17, $P=0.03$; Table S1b) and nearer to the forest edge (Z=−2.06, $P=0.04$). Neither nest habitat nor its distance to the forest edge affected the predation rate by mesocarnivores. Proportion of agriculture in the landscape did not affect scent post visits and was omitted in model selection (Table S1c). Distance to the nearest supplemental feeding site in wild boar areas associated negatively with the number of mesocarnivore visits (Z=−2.38, $P=0.02$; Table S1d) but did not significantly affect the nest predation probability (Z=−1.3, $P=0.19$).

Discussion

Our study, conducted within a low-density wild boar area, shows that the effects of wild boar on artificial nest predation rates were modest. However, our results indicate that the wild boar may have a negative effect on mesopredator abundances. While the rates of actual nest predation cannot be reliably inferred from artificial nest experiments due to human placing choice and deterring effects (e.g., scent, camera traps), they provide an index for comparing spatial and temporal differences in predation rates and predator communities. Previous research also indicates that real ground nests are predated predominantly by mammalian predators (Macdonald and Bolton 2008), while corvid predation may be positively biased in camera trap studies (Henden et al. 2024), further justifying our focus on mammals.

Direct nest predation of the wild Boar

As expected, wild boars predated some nests, but their predation pressure was negligible. The observed predation from wild boars in this study, at just 3%, is notably lower than the 35–41% range reported in Central and Southern Europe (Svobodová et al. 2012; Carpio et al. 2014; Senserini and Santilli 2016; Mori et al. 2021) and 18% in Sweden (Carpio et al. 2016). This indicates that the nest predation pressure of wild boar within the current Finnish population is relatively small. As evidenced by Svobodová et al. (2012), the risk of wild boar predation on nests is undoubtedly related

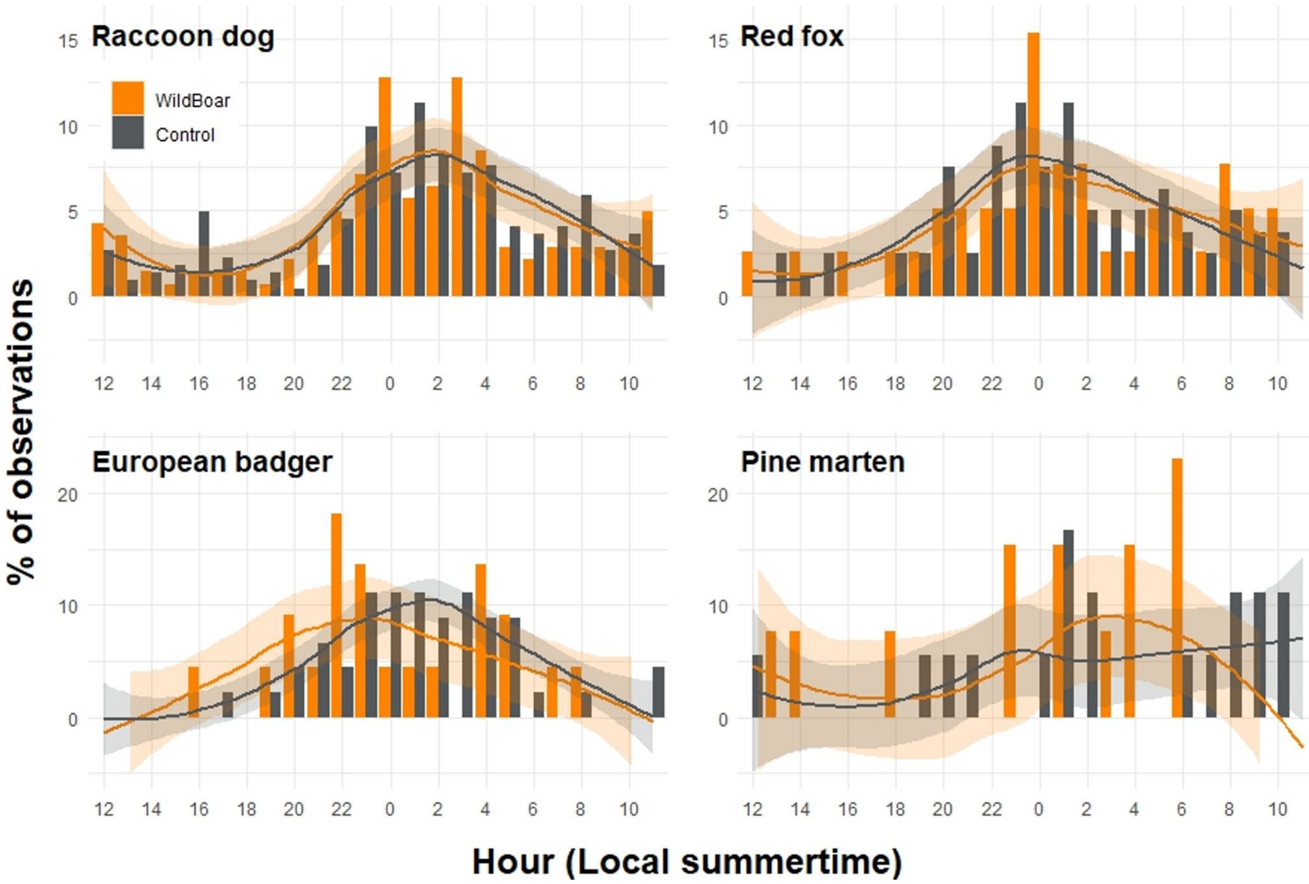

Fig. 3 Mesocarnivore activity as the proportion of observations per hour of the day (accompanied with Loess smoothers as lines with 95% confidence bands) in wild boar sites and control sites

to the abundance of boars. In many Central and Southern European research areas, densities vary between 200 and 1700 wild boars/100 km^2 (ENETWILD-consortium (2022), while the wild boar hunting bag in the Swedish study area alone was up to 80 individuals per 100 km^2 (Carpio et al. 2016). In Finland, the highest wild boar densities are currently 30–50 wild boars per 100 km^2 (Ruha and Kunnasranta 2024). In addition to the lower likelihood of wild boars in nest vicinities, lower densities may be associated with larger home range sizes in the northernmost edge of the species' distribution (Miettinen et al. 2023), which in turn decreases wild boar searching effort and foraging pressure per unit area.

Wild boar foraging behaviour may also be influenced by other available food sources. Most of the artificial nests in the wild boar areas occurred near the Finnish–Russian border, where wild boars have distinctive movement patterns between day-rests on the Russian side and nightly foraging excursions into Finnish crop fields and supplemental feeding sites (Miettinen et al. 2023). Thus, foraging hotspots (that provide a reliable food source for the whole group) may divert wild boars from seeking scarce, small-scale food items in the landscape (e.g. bird nests). In our study, the data were insufficient for analysing the risk of wild boar nest predation in relation to the proximity of supplement feeding sites or other food sources. Elsewhere, supplemental feeding has been shown to divert wild boar movement (Calenge et al. 2004; Cellina 2008; Muthoka et al. 2022) but to also increase nest predation (Selva et al. 2014; Oja et al. 2015). Feeding may also promote wild boar population growth (Geisser and Reyer 2004; Cellina 2008), leading to increased local density and higher risk of wild boar predation. Thus, the effects of other food sources on nest survival may be either positive or negative.

Indirect effects of wild boars

In addition to the direct predation pressure, Carpio et al. (2016) suggested that wild boars may also promote nest survival by deterring other mammalian predators. We found that relative mesopredator abundance was lower on wild boar sites (based on scent post visits). However, wild boars did not influence the number of mesocarnivore visits at nests or the timing of activity peaks of these species. Overall, the risk of mesopredator predation was not higher in the control sites. The deterrent effect of wild boar presence on mesocarnivore abundance was observable only at scent posts. The numbers of mesocarnivore predation events (27) and nest visits (156) are considerably smaller than the number of visits at scent posts (327). This demonstrates the strong effect and reach of the lure (compared to eggs at nests), highlighting the differences in observation efficiency. Even though the proportion of mesocarnivores was higher in control sites with all three methods, wild boar presence may have such small intraguild effects that only scent post observations had sufficient sample size to exhibit it statistically. Furthermore, the low density of wild boars in our study area could diminish the avoidance effects of mesocarnivores that might otherwise be expected.

Alongside the presence and absence of wild boars, other factors may also affect the results. Supplemental feeding benefits and lures mesocarnivores in addition to the ungulates that the feeding actually targets (Kauhala et al. 2022). In our study, mesocarnivore activities at the nest sites indeed increased nearer the feeding sites, but no effects on nest predation pressure were observed. Carpio et al. (2016) stated that the deterring effect of wild boars may result from differences in landscapes and habitat preferences of the predators. The main landscape feature differing gradually within our study area is the proportion of agricultural fields. Our analysis showed that the proportion of agriculture in the landscape increased mesocarnivore predation and the number of their visits to nests. This may reflect the role of agriculture in the spatial behaviour of mesocarnivores (especially raccoon dog and badger; Holmala and Kauhala 2009; Kauhala and Auttila 2010), which may also affect nest predation pressure (Chalfoun et al. 2002; Holopainen et al. 2024c). However, our results indicate that wild boars may have some effect on mesocarnivores regardless of the landscape: on a larger spatial scale (habitats within reach of the scent posts), agriculture was not correlated with relative mesocarnivore abundance, whereas wild boar presence was.

In addition to spatial abundance, wild boars may potentially affect the temporal behaviour of mesocarnivores. As shown by Osugi et al. (2019), mesocarnivore activity is expected to shift away from wild boar activity peaks, which in our study area occur directly after sunset (around 21:00 local summertime in the study season; Miettinen et al. 2023). In this study, we did not find evidence for such changes in activity patterns on a landscape level. However, avoidance may occur locally in stable common foraging hotspots (see Osugi et al. 2019) such as supplemental feeding sites (e.g., Saldo et al. 2024). Spatially more scattered ground nests and brief scent post experiments may be unlikely to elicit temporal avoidance behaviours of mesocarnivores towards wild boar presence. Furthermore, as the wild boar has only recently settled in the research area, the temporal avoidance patterns may not yet have had sufficient time to evolve among the mesocarnivore species.

Conclusions

Our results suggest that wild boars can be potential nest predators of ground-nesting birds, but the effect is relatively minor with the current low wild boar densities in Finland. We also found that wild boar may, to some extent, deter mesocarnivores, thus promoting nest survival. Overall, both resulting negative and positive effects of wild boars on the survival of nests appear modest in the current conditions. Nonetheless, the study provides a baseline for monitoring the interactive role of wild boars as members of the mammalian community in Northern Europe. Wild boar dispersal and survival are predominantly restricted by harsh winter climates (Markov et al. 2019). Due to climate change, the wild boar population will likely continue to grow and spread in northern latitudes, which could alter their ecological role and interactions with other species in the future.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10344-025-01991-8.

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Author contributions EM, SH, HK, and V-MV contributed to the study conception. All authors (EM, SH, OH, HK, MK, and V-MV) participated in further planning the study design. EM, HK, and V-MV contributed to data collection. Analysis was conducted by EM and SH, and the first draft of the manuscript was prepared by EM. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets used and analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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