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RESEARCH

Mesopredator control for waterfowl conservation: hunting reduces invasive raccoon dog abundance and predation on artificial nests

Vesa Selonen[1] · Purabi Deshpande[1] · Kari Karhula[4] · Andreas Lindén[3] · Mikko Toivola[2] · Toni Laaksonen[1]

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Abstract

The use of predator control as a conservation tool, for example to protect ground-nesting bird populations, remains a subject of ongoing debate. To justify the control or eradication of a predator, managers need to provide evidence on the success of the program. We evaluated the effectiveness of a raccoon dog control program (2021–2024) organized by governmental bodies around wetlands important for waterfowl conservation in Finland. The raccoon dog is an invasive species and a nest predator of waterfowl. We assessed control effectiveness by analysing how hunting methods and effort influenced catch and how varying hunting intensity across wetlands affected raccoon dog abundance measured with camera-traps. There was a moderate negative relationship between previous hunting efforts and monthly catch, indicating diminishing returns, but full eradication was not achieved. Among the four used hunting methods, hunting from dens proved the most efficient hunting method in relation to time used. The impact of catch on the subsequent number of camera-trap observations varied. Winter camera-trap data from feeding sites showed no decline in raccoon dog presence, potentially due to autumn immigration. However, hunting success showed a negative effect on raccoon dog camera-trap observations in spring (waterfowl breeding season), suggesting a substantial, but incomplete, raccoon dog population reduction. Consistent with this, raccoon dog predation of artificial nests decreased, without compensatory increases by other predator species, resulting overall in reduced nest predation. We conclude that control efforts reduce raccoon dog numbers and potentially benefit wetland bird species, but long-term success requires substantial and sustained effort.

Keywords Invasive species · Nest predation · Conservation · Management · Hunting · Wetland

Introduction

An increase in the abundances of generalist predators, particularly of invasive species, can lead to declines in prey populations (Genovesi 2005; Salo et al. 2007; Wallach et al. 2015; but see e.g. Wallach and Lundgren 2025). When an endangered prey is involved, a common intervention is the control of predators (Reynolds and Tapper 1996; Doherty and Ritchie 2017). However, control measures are often laborious and comprise ethical issues regarding animal rights and welfare (Genovesi 2005). Mixed views exist on the effectiveness of predator control (e.g. Bolton et al. 2007; Holt et al. 2008; Fletcher et al. 2010; Smith et al. 2010). Some authors suggest that the hunting of predators never directly saves the targeted prey animal (Treves et al. 2019) and is failing in the absence of sustained predator suppression (Lennox et al. 2018). Lethal control also is negatively perceived by an increasingly large portion of the public with demands of a conservative approach in its application (Treves and Naughton-Treves 2005; Comte et al. 2017). Indeed, alternative methods of reducing predator pressure, such as habitat improvement enabling avoidance of predators by prey (Chalfoun et al. 2002) or other methods aiming to prevent predation events such as chemical camouflage or conditioned food aversion have gained support (Selonen et al. 2022; Gautschi et al. 2024). Despite this debate, there is considerable proof that carefully planned predator control

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✉ Vesa Selonen
vessel@utu.fi

[1] Department of Biology, University of Turku, Turku FI-20014, Finland

[2] Finnish Wildlife Agency, Piikkiö FI-21500, Finland

[3] Natural Resources Institute Finland, Helsinki FI-00790, Finland

[4] Parks & Wildlife Finland, Oulu FI-90130, Finland

is an effective conservation measure (Smith et al. 2010; Lazure and Weladji 2024).

Consensus seems to be that short-term control programs are typically doomed to fail, because culled predators are rapidly replaced through immigration (Newsome et al. 2014; Lieury et al. 2015; Minnie et al. 2016; Lennox et al. 2018). In particular, full eradication of predators needs long-term planning and execution, and managers need to provide data on the effectiveness and usefulness of predator control. However, it is still largely unclear what is the effort needed for successful predator eradication or control. A recent review on mesopredator control programs (Lazure and Weladji 2024) concluded that data for different control methods is limited, shooting being an understudied method, while trapping or use of poisons showed clearer positive effects (Lazure and Weladji 2024). Indeed, some earlier control programs concluded that shooting may be an ineffective method for foxes (McLeod et al. 2011), but, for example, the use of GPS-devices on the hunting dogs may increase effectiveness of modern shooting programs.

A particular problem related to mesopredators is the increased nest predation that may have contributed to population declines of ground-nesting birds across Europe (Roos et al. 2018; McMahon et al. 2020). For example, in Finland, the populations of many waterfowl species have declined in just a few decades, with some species declining as much as two-thirds or even 90% since the late 1980’s (Laaksonen et al. 2019), with half of the examined species declining to less than half of their previous populations (Piha et al. 2024). Increasing mesopredator populations are suggested to play a major role in these declines (Nummi et al. 2019). A particular concern is related to alien mesopredators that will create additional predation pressure to that of native predators (Directorate-General for Environment 2022). The most common invasive mesopredator in large parts of Europe is the raccoon dog (*Nyctereutes procyonoides*; Kauhala and Kowalczyk 2011). It is a nest predator of ground nesting birds (Dahl and Åhlen 2019; Holopainen et al. 2021), and in wetlands it preys on amphibians (Tuomikoski et al. 2024) that are a globally declining taxon (IUCN 2009).

We used data from a large-scale control project aiming to remove raccoon dogs from areas surrounding 71 wetlands important for waterfowl conservation in Finland. The project started in autumn 2021 and has continued since then. It is part of Helmi-program by Finnish Ministry of Agriculture and Forestry and Ministry of the Environment, one aim of which is to improve the conservation of endangered waterfowl that are potentially threatened by nest predation by invasive predators. The Finnish government has put a substantial amount of resources on this project and its effectiveness needs to be evaluated. The study system is unique in the sense that the effort and success of the raccoon dog hunt varies in different wetlands, allowing us to interpret the effect of varied hunting pressures on the abundance and nest predation (tested with artificial nests) by the raccoon dog.

First, we studied (i) how the time used for hunting affects the catch, with the aim to evaluate the needed effort. We also analyse how the catch varies with time used for different hunting methods (traps vs. shooting done with three different approaches). Next (ii) we explored how effectively the control program has succeeded in removing raccoon dogs. For this, we utilized (a) camera-trap data and (b) artificial duck nest data from three years, to analyse the effect of hunting success on the raccoon dog abundance and potential nest predation level. Artificial duck nests were used in a subset of 12 study wetlands. For camera-trap data, we had data (1) from all 71 study sites with “feeder cameras” mainly in winter at feeding sites maintained for hunting and, (2) from a subset of 31 study sites with “spring cameras” used particularly for monitoring raccoon dogs near the wetlands during the breeding season of waterfowl. We expected that if the control of raccoon dogs is effective, increased catch (number of killed raccoon dogs preceding the camera observations) decreases the subsequent number of raccoon dog camera-trap observations and decreases predation of artificial nests. We also expected the presence of raccoon dogs to decrease over time following the start of the control program. We discuss how our results can be used to improve this program in its future efforts.

Materials and methods

Study species and study areas

The raccoon dog is an omnivorous canid that weighs typically 5 kg in early summer and about 9 kg in autumn (Kauhala 1993). It is monogamous, denning in pairs and can produce litters of up to nine offspring each year, starting at the age of one year. The average size of raccoon dog home range in southern Finland is 400–1100 ha (Toivonen et al. 2024). Home ranges can partially overlap between several individuals, especially outside the breeding season (Kauhala and Kowalczyk 2011). Raccoon dogs may use winter sleep during the coldest periods but remains active in mild winter weather (Mustonen and Nieminen 2018; Selonen et al. 2024c). The winter nests of raccoon dogs in Finland are typically underground burrows often made by badgers or red foxes, or dens under barns, cottages or rocks. The raccoon dog spread to Finland in the 1950s from former Soviet Union, where it was introduced for fur production and hunting. The current European range of the species is mainly Eastern and Northern Europe, Germany and Denmark (Kauhala and Kowalczyk 2011), and it is expanding

(Selonen et al. 2024b). In Finland, the distribution of raccoon dog covers most of the country excluding the northern subarctic parts (Selonen et al. 2024b). In the southern parts of the country, it currently seems to be the most common mesopredator (Selonen et al. 2024a).

The study was carried out in boreal managed forest landscape surrounding wetlands crucial for waterfowl conservation. The landscape in these areas is dominated by mainly managed coniferous and mixed forests, the main tree species being the Scots pine (*Pinus sylvestris*), the Norway spruce (*Picea abies*), and birches (*Betula* spp.). Water bodies and agricultural lands fragment the forested landscape. While agricultural and urban areas are concentrated to southwestern and southern Finland, they are sparsely distributed throughout the country.

To account for regional climatic variation across Finland, specifically from the northeast to the southwest coastal areas, we used the length of the growing season (in days, provided by Statistics Finland) as a proxy for the climate gradient. Colder temperatures, longer winters, and a correspondingly shorter growing season characterize the climate in the northeast with less productive habitats and lower density of raccoon dogs (Selonen et al. 2024b).

Hunting of raccoon dogs

We utilize data on hunting effort (hours spent hunting), hunting method (traps vs. shooting done with three different approaches), catch (numbers of removed raccoon dog individuals), raccoon dog abundance (measured with camera-traps) and on the possible impact of control measured as the rate of predation on artificial ground nests.

Raccoon dog hunting was conducted around 71 wetlands (hereafter referred to as “hunting area”) in Finland (Fig. 1). Each hunting area, with an average land area size of 65 ± 45 km^2 (SD; range 1.3–213 km^2), encompassed a wetland or

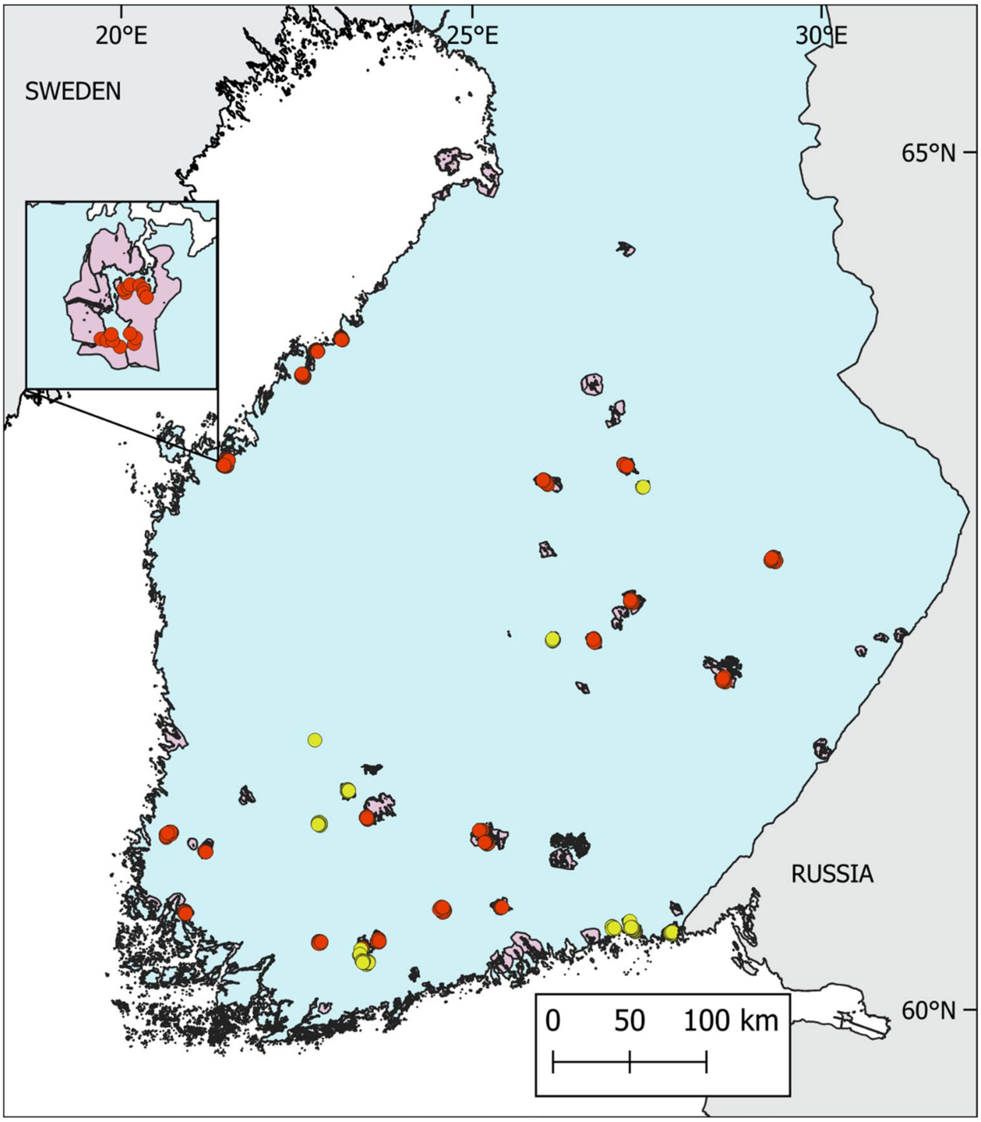

Fig. 1 Location of wetlands and hunting areas ($n = 71$) used to study effectiveness of hunting for controlling invasive raccoon dogs in Finland (2021–2024). Hunting areas are shown with pink shapes. Red and yellow dots are cameras in wetlands used for spring camera survey ($n = 31$), of which the latter denote the wetlands ($n = 12$) where artificial nest study was also conducted. The inset map shows an example of a wetland and hunting area with spring camera locations surrounding the wetland (red dots)

lake targeted for waterfowl conservation (hereafter referred to as “wetland)”. The size of the wetlands varied (mean 490 ± 1100 SD ha; range 43–11823 ha). The hunting area, where hunting activities occurred, surrounded the wetland. It was aimed to be large enough so that both raccoon dogs living immediately adjacent to the wetland and those in nearby areas that potentially might immigrate to the wetland would be eradicated. Within the wetland, the hunt was often complicated due to water and dense vegetation such as reed beds, although it is part of the hunting area. The home ranges of raccoon dogs can be only partially in the wetland, but in spring and summer the wetland habitat is preferred by the raccoon dog (Toivonen et al. 2024). Thus, as the control measures empty home ranges near the wetland, those can soon be recolonized by the individuals living nearby. In some cases hunting areas were likely too small to effectively prevent immigration. Despite this, the size of hunting area had only modest effect on catch (see results). Immigration coming outside the hunting areas occurs mainly each autumn, when is the main dispersal period of the species (Kauhala and Kowalczyk 2011).

Hunting activities started in autumn 2021 and have continued uninterrupted since then with lesser activity in summer and mid-winter than in autumn and spring. For year 2021, we had data for total used hunting hours and total catch of raccoon dogs. Starting from January 2022 we had monthly catch numbers until May 2024. Catch numbers increased in autumn (dispersal season of raccoon dogs), but the data was limited to properly compare seasonal effects of hunt and we mainly use annual catch numbers in our analysis. For hunting hours, we had monthly data from January 2022 until the end of 2023.

An average of 5.5 ± 2.0 (SD) trained hunters participated in the hunt within each hunting area. This was on average 0.4 person-years of paid work and 0.2 person-years as volunteer work in total per each hunting area per year. The number of hunters was aimed to be larger for larger hunting areas, and this aim succeeded at some level, as there was a positive correlation between hunting hours and hunting area size ($r^2 = 0.22$; on average there were 0.02 ± 0.03 person-years of work per km^2). Hunting groups employed four methods: trapping and three types of shooting (hunting with baying dog, den hunting, and stand hunting from feeders). Trapping involved an average of 12 live traps (kanu-trap) per hunting group. The size of these traps is 150 × 100 × 50 cm and they were baited with food, typically carcass parts of deer or moose, fish, or dog pellets. Hunting with baying dog involved hunters locating and shooting active raccoon dogs with the aid of tracking dogs, usually starting from feeding sites after the presence of raccoon dogs was confirmed by wildlife cameras. Den hunting targeted raccoon dogs in their winter dens. Dogs were used to locate individuals within the cavities, from which they were then retrieved and shot. Stand hunting involved shooting raccoon dogs at feeding sites (carcasses or other bait), wildlife cameras were also used in this method to locate actively used feeding sites.

The hunting groups reported how many hours they used for each hunting method (Supplementary Table 1). For trapping, the reported hours included the time used for setting up the trap and baits and visits to the trap. The total number of raccoon dogs killed (catch) was reported monthly, but not separately by each hunting method for which we had only the data for time used.

Recording raccoon dog abundance from camera traps

Wildlife cameras (Burrel S12 or Uovision UV595) were used to estimate raccoon dog abundance in two different set-ups as follows.

a) Feeder cameras were deployed in all 71 hunting areas during early winter to early spring to support baying dog and stand hunting. Of these, 65 areas were monitored for three years, three areas for two years, and three areas for a single year. Each camera was positioned near a carcass or feeding site to aid hunters in locating raccoon dogs. It is important to note that we did not have information about the locations of individual feeder cameras and hunting groups in few cases could also relocate a camera if no raccoon dogs were detected. This was not common (less than 5% of cases) and usually cameras were in single location, but does create a possible bias to feeder-camera data that may underestimate occurrence of zero observations. We are unable to evaluate the exact level of this bias, but if the hunters managed to eradicate all raccoon dogs there does not exist this bias, as there are no raccoon dogs in the area. However, for estimating slight changes in raccoon dog numbers the data from “spring cameras” is likely more reliable.
The low number of cameras used per hunting area (on average 5 ± 2 SD) suggests that observations from each feeder camera were likely independent. The cameras were 5–10 m from a feeder or carcass. At this distance, it was easy to identify raccoon dogs from camera trap photos. Feeders typically contained grain, apples, and dog pellets, and carcasses were often leftover from deer or moose hunts. The type of attractant used did not influence the number of raccoon dog observations (Selonen et al. 2024c). Photos were checked for all days during on average 8.9 ± 3.1 days period for November/December, for March and for April. This observation period length was chosen to manage the large volume

of photos and was accounted for during data analysis. There was variation in the period length because we aimed for 10-days period but sometimes a camera was on for shorter time. Raccoon dogs in the photos were counted, with observations within a 30-minute period considered a single individual (following previous studies, e.g., Holopainen et al. 2021; Selonen et al. 2022).

b) In spring, in late May, an additional camera survey was conducted at 31 of the wetlands. For this survey, an average of 11.5 cameras per wetland were placed in the shoreline forests and were active and checked for photos for 17.6 ± 6.7 days per camera. The observation period was longer than in a) to ensure enough observations, as we did not use attractants for this survey, thus cameras captured more "natural" raccoon dog activity levels, compared to the feeder camera setup, described above. Two wetlands were sampled only in 2024. The camera locations were predetermined and remained fixed throughout the study period. Cameras were positioned 10–100 m from the shoreline, within the forested areas. Some waterfowl species nest in these shore forests, while others nest within the wetlands themselves, where camera placement was not feasible. Cameras were spaced 200–300 m apart and aimed to provide comprehensive coverage of the wetland perimeter. Similar to feeder cameras, observations within a 30-minute period were considered a single observation. Given the raccoon dog's generalist habitat use (Toivonen et al. 2024) and our previous finding of no habitat effect on raccoon dog camera observations near wetland areas (Selonen et al. 2022), habitat was not included in the current analysis.

c) Finally, from late May to early June, the leaders of the hunting groups placed a total of 257 artificial nests at 12 wetlands (on average 9 ± 2 (SD) per wetland, across the years 2022–2024). These wetlands overlapped with those used in the spring camera survey (b). The artificial nests were constructed from grass and mallard feathers and each contained one farmed mallard egg. A camera trap taking photos, positioned 3–5 m from each nest so that the egg was visible in the images, recorded the species likely responsible for predation. While actual predation events were often not captured, the presence of animals near the nest was used to identify the likely predator. The artificial nests remained in the field for approximately one week. While shorter than the typical three-to-four-week incubation period of the focal waterfowl species, this one-week deployment provides an index of predation pressure within the study sites, which have previously been shown to exhibit high predation rates (e.g., Holopainen et al. 2021; Selonen et al. 2022).

Statistical analyses

Statistical analysis were performed using R version 4.4.1 (R Core Team 2024). Because our response variables were in the form of counts, we used negative binomial error structures in our models to avoid overdispersion problems and to ensure positive estimates. The models have log link functions. We checked that the residuals of the models met the assumptions of GLMMs using the DHARMa package (Hartig 2024).

Catch and time use analyses

We analysed the relationship between annual catch (number killed) and annual hunting effort (time used) using a generalized linear mixed models using the 'glmmTMB' package (Brooks et al. 2017). The annual catch of raccoon dogs at each area was the response variable (negative binomial distribution). We built a model with the fixed effects: the total annual hunting time (hours) per hunting area, the size of the hunting area (km^2), the length of the growing season in the area, and year (as a categorical variable with two levels). For this analysis, only data from years 2022 and 2023 were used, because hunting had not properly started at all sites in 2021, and 2024 data is only for the first half of the year. Hunting area ID was included as a categorical random effect (71 levels).

To assess the relative contribution of each hunting method to overall catch, we constructed four additional models. These models were identical to the initial model described above, except that the annual area-specific total hunting time was replaced as log transformed offset and the proportion of time spent using an individual hunting method was included in the model. That is, proportion of time used for trapping, hunting with baying dog, den hunting, and stand hunting from the total time used was explanatory variable in separate models, because these obviously were correlated with each other.

For monthly catch, we analysed how the all previous hunting effort affected current catch (catch in each month during the program). We built a negative binomial model where monthly catch (each month of years 2022 and 2023) was explained with total hunting hours preceding the catch (sum of hunting hours between start of the program in autumn 2021 and the month in question; year 2024 was omitted because we did not have monthly hunting hours for 2024). Length of growth season was fixed effect and hunting area (71 areas) and season (four-levels: spring, summer, autumn, and winter; the monthly catch was highest in autumn and lowest in summer) were included as random effects in the model. The log-transformed hours hunted in the current month (dependent variable) was included as an offset. This was done to control for the effort in a given month as we were interested here on the effect of effort preceding the month.

Camera data and artificial nest analyses

a) Feeder camera data: Raccoon dog observations from feeder cameras (the sum of observations per camera per wetland in a given year; *n* = 71 wetlands) were modelled using a negative binomial distribution. We used the catch (number of raccoon dogs hunted in previous year per 1000 ha per month, i.e. as an average over months) as the primary explanatory variable. The previous year's catch was used, because it is likely that current year observations are influenced by prior hunting pressure. The length of the growing season was also included as a continuous fixed effect. Month of camera observation (November–April) was included as a random effect to account for seasonal variation in raccoon dog activity levels (Selonen et al. 2024c). A nested random effect of camera within hunting area was included to account for repeated observations. The log-transformed number of days the camera was active was included as an offset.

b) Spring camera data: To analyse effect of catch on spring camera observations of raccoon dogs, we constructed a similar negative binomial model (*n* = 31 wetlands) as described above. Explanatory variables included the number of raccoon dogs hunted (per 1000 ha) in the previous year and the number hunted in the current year (February to May). Catches were calculated as average over the months. We included current year hunting numbers because we hypothesized that hunting immediately preceding the spring camera survey would have the greatest impact on raccoon dog observations (current and previous year hunting numbers were only moderately correlated). Month was not included, as observations were made in one period in May. Otherwise, the random effect structure and offset remained the same as in model (a).

c) Artificial Nest Predation Data: We analysed the effect of catch on artificial nest predation by raccoon dogs (*n* = 12 wetlands). Predation events were coded as 1, and the absence of predation during the observation period was coded as 0. We then constructed a binomial model with predation as the response variable. Explanatory variables were the catch (number of raccoon dogs hunted per 1000 ha per month) in the previous year, the catch from February to May of the current year (per 1000 ha per month), the length of the observation period and the length of the growing season. A nested random effect of camera within wetland was used to account for repeated sampling.

Because the control program had a clear start, we wanted to show the effects in time. To do this, we analysed changes over years, by building additional models for the analyses a), b), and c) described above. These models were similar to those described above, but catch numbers were removed and replaced with year as a categorical variable. This was done because the catch was dependent on year of the study. Additionally, for the artificial nest predation analysis (c), four separate models were constructed to examine the effect of year on predation by: (1) all predators, (2) raccoon dogs, (3) mesopredators other than raccoon dogs, and (4) corvids. We then did post hoc comparisons using the 'contrasts' command of the emmeans package (Lenth 2024) to assess the effects of consecutive years. Finally, we also tested whether predation of artificial nests by raccoon dogs was related to raccoon dog observations in spring cameras. For this, we built a binomial events/trial model where the event was nests predated by raccoon dogs and the trial number of all nests in a wetland in one year. We applied a logit link function. The relative abundance index (camera observations per 100 camera days) of raccoon dogs in a wetland in spring cameras in a given year was the explanatory variable. Wetland ID was included as a random effect on the intercept.

Results

Raccoon dog catch and hunting effort

The annual catch (number of hunted raccoon dogs 2022 and 2023) increased with hunting effort (time used; Table 1A; Fig. 2A) and decreased from 2022 to 2023 (Table 1A). The catch increased with increasing hunting area and with longer

Table 1 (**A**) Factors affecting annual catch (number of raccoon dogs hunted) in 71 hunting areas (random effect) in Finland during 2022 and 2023 (*n* = 139; R^2c lognormal = 0.63, R^2m lognormal = 0.18) modelled with negative binomial error distributions. the intercept represents year 2022. (**B**) Results for how the time spent on different hunting methods explained the total annual catch. these models were identical in structure to model (**A**), but total hunting hours were replaced as offset (log) and the proportion of hours (from total hours) used for the different hunting methods were the explanatory variable in separate models (full models not shown)

A. Hunting methods pooled*	Estimate	SE	Z-value	*p*-value
Intercept	**–10.005**	**1.677**	**–5.99**	**< 0.001**
Hunting hours	**0.00063**	**0.00025**	**2.53**	**0.01**
Hunting area, km^2	**0.0066**	**0.0026**	**2.50**	**0.01**
Length of growing season	**0.0758**	**0.0097**	**7.79**	**< 0.001**
Year (2023)	**–0.155**	**0.055**	**–2.80**	**0.005**
B. Different hunting methods separately*				
Proportion of den-hunting	**0.96**	**0.49**	**1.94**	**0.05**
Proportion of stand-hunting	−0.83	0.45	−1.84	0.07
Proportion of baying-dog	−0.10	0.36	−0.29	0.77
Proportion of trapping	0.04	0.31	0.12	0.90

AIC values for different models, den-hunting hours 1284, stand-hunting hours 1284, baying-dog hours 1288, trap hours 1288. Variables with significant p-value are in bold

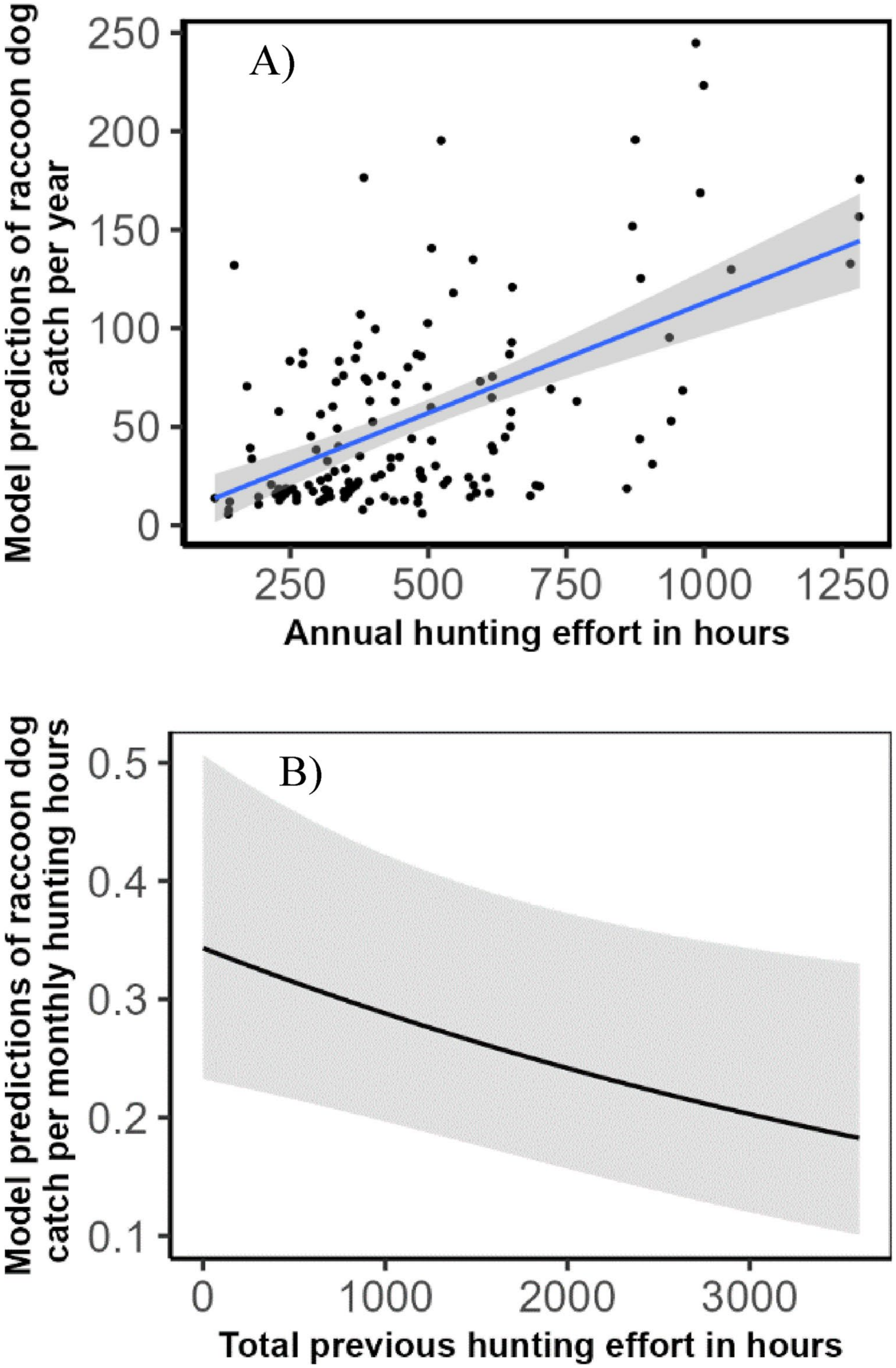

Fig. 2 Relationship between (**A**) annual catch of invasive raccoon dogs (*n* = 71 wetlands for 2 years: total *n* = 139, as for three wetlands we had data for only one year) and the annual hunting effort during the same year (measured in hours). Points are the predicted values and line the predicted trend. (**B**) Monthly catch of raccoon dogs (per hunting hours of the month) in relation to the total previous hunting effort near wetlands in Finland during 2022 and 2023

growing seasons (Table 1A). When proportion of time used for the four different hunting methods were included as explanatory variables, the models incorporating den hunting and stand hunting best explained the total catch (lowest AIC), the catch increasing with increasing proportion of den hunting from all hunting and decreasing with increasing proportion of stand-hunting (marginally non-significantly; Table 1B).

For monthly catch, the preceding effort (total hunting hours since start of the program) was negatively related to monthly catch, i.e. higher previous effort resulted in diminishing monthly catches (Fig. 2B; estimate:

Table 2 (**A**) Factors affecting raccoon dog observations in wildlife cameras in November-April in "feeder cameras" in 71 hunting areas (random variables) during 2022–2024 ($n = 2385$) modelled using negative binomial error distributions. Catch is the number of killed raccoon dogs as an average over months and per 1000 ha. (**B**) Yearly changes in observations with post hoc comparisons using the contrasts command of the emmeans package

(A)	Estimate	SE	Z-value	*p*-value
Intercept	**–17.93**	**2.47**	**–7.26**	**< 0.001**
Catch previous year	–0.11	0.08	–1.32	0.19
Length of growing season	**0.093**	**0.01**	**6.54**	**< 0.001**
(B) Contrast				
2023–2022	–0.22	0.10	–2.18	0.056
2024–2023	**0.46**	**0.15**	**3.12**	**0.004**

Variables with significant p-value are in bold

Table 3 (**A**) Factors affecting raccoon dog observations in wildlife cameras in late spring (May/June: "spring cameras") in surroundings of 31 wetlands (centre of hunting area; random variable) during2022–2024 ($n = 1014$) modelled with negative binomial error distribution. Catch is the number of killed raccoon dogs as an average over months and per 1000 ha. (**B**) Yearly changes in observations with post hoc comparisons using the contrasts command of the emmeans package

(A)	Estimate	SE	Z-value	*p*-value
Intercept	**–24.32**	**5.48**	**–4.44**	**< 0.001**
Catch previous year	**–0.78**	**0.18**	**–4.27**	**< 0.001**
Catch current year (Feb–May)	**0.017**	**0.006**	**2.84**	**0.004**
Length of growing season	**0.12**	**0.03**	**3.74**	**< 0.001**
(B) Contrast				
2023–2022	**–0.96**	**0.17**	**–5.61**	**< 0.001**
2024–2023	–0.06	0.19	–0.29	0.94

Variables with significant p-value are in bold

-0.00018 ± 0.00008, z = -2.24, $p = 0.02$; full model in Supplement Table 2).

Raccoon dog observations

a) Feeder camera observations: Cameras recorded an average of 3.1 ± 6.4 (SD) raccoon dog observations during each of three separate approximately 9-day sampling periods during winter/early spring months (total sampling period 27 days, $n = 71$ hunting areas and 622 cameras).

There was no obvious relationship between the catch from the previous year and the raccoon dog observations at feeders in winter, but observations increased with increasing length of growing season i.e. from north-eastern to south-western wetlands (Table 2A). There was a decreasing (non-significant) trend in raccoon dog observations from 2022 to 2023, followed by an increase from 2023 to 2024 (Table 2B).

b) Spring camera observations: Each camera recorded an average of 0.8 ± 2.2 raccoon dog observations during on average 17.6 days observation period during the prey breeding season (31 wetlands and 374 cameras).

Raccoon dog observations in spring decreased with increasing catch in the previous year (Table 3A, Fig. 3A). However, catch in the current year (February–May i.e. before the prey breeding season) was positively associated with raccoon dog observations (Table 3A). Observations increased with increasing length of the growing season (Table 3A). Yearly changes showed a decrease in raccoon dog observations from 2022 to 2023, remaining at the low level for 2024 (Table 3B; Fig. 3C).

c) Artificial nest predation: For 257 artificial nests across the three sampling years and 12 wetlands, we observed 152 predation events by nine different predator species. Identified predators included hooded crow ($n = 39$ events), raccoon dog ($n = 35$), red fox ($n = 21$), badger ($n = 18$), magpie ($n = 15$), Pine marten ($n = 9$), deer sp. ($n = 4$), Marsh harrier ($n = 2$), crane ($n = 2$), and unknown species ($n = 7$). Yearly numbers of non-predated nests were 12 out of 69 (17%), 37 out of 67 (55%), and 56 out of 121 (46%), in 2022, 2023 and 2024 respectively.

Nest predation events by raccoon dog decreased with higher catch in the previous year (Fig. 3B). Catch in the current year and the length of growing season had no effect (Table 4.A). Yearly changes showed a decrease in raccoon dog nest predation probability from 2022 to 2023, with predation rates remaining low in 2024 (Fig. 3C). An overall decline observed in nest predation was driven primarily by a decrease in raccoon dog predation, as no significant yearly differences were found for predation by other predators (Table 4.B). Predation of artificial nests by raccoon dogs was positively related to their abundance in spring cameras in the 12 study wetlands (estimate 0.11 ± 0.02, $F_{1,24} = 19.0$, $p = 0.0002$).

Discussion

We observed that full eradication of raccoon dogs was not achieved in any of the control project wetlands. There was indication of diminishing returns of monthly catch with increased hunting pressure, but catch rates remained above zero throughout the program and annual catch increased linearly with the used effort. Hunting method effectiveness varied, as indicated by time spent on shooting from dens being most directly related to the total catch. Camera-trap data showed a varied response to hunting success: while winter observations at feeder cameras showed no clear reduction in raccoon dog presence, a significant decline was observed during the waterfowl-breeding season (spring cameras). A corresponding decline was seen in a reduction in raccoon dog predation events on artificial duck nests. Importantly, this reduction in nest predation was not compensated by increased predation from other species, resulting in a net decrease in overall artificial nest predation.

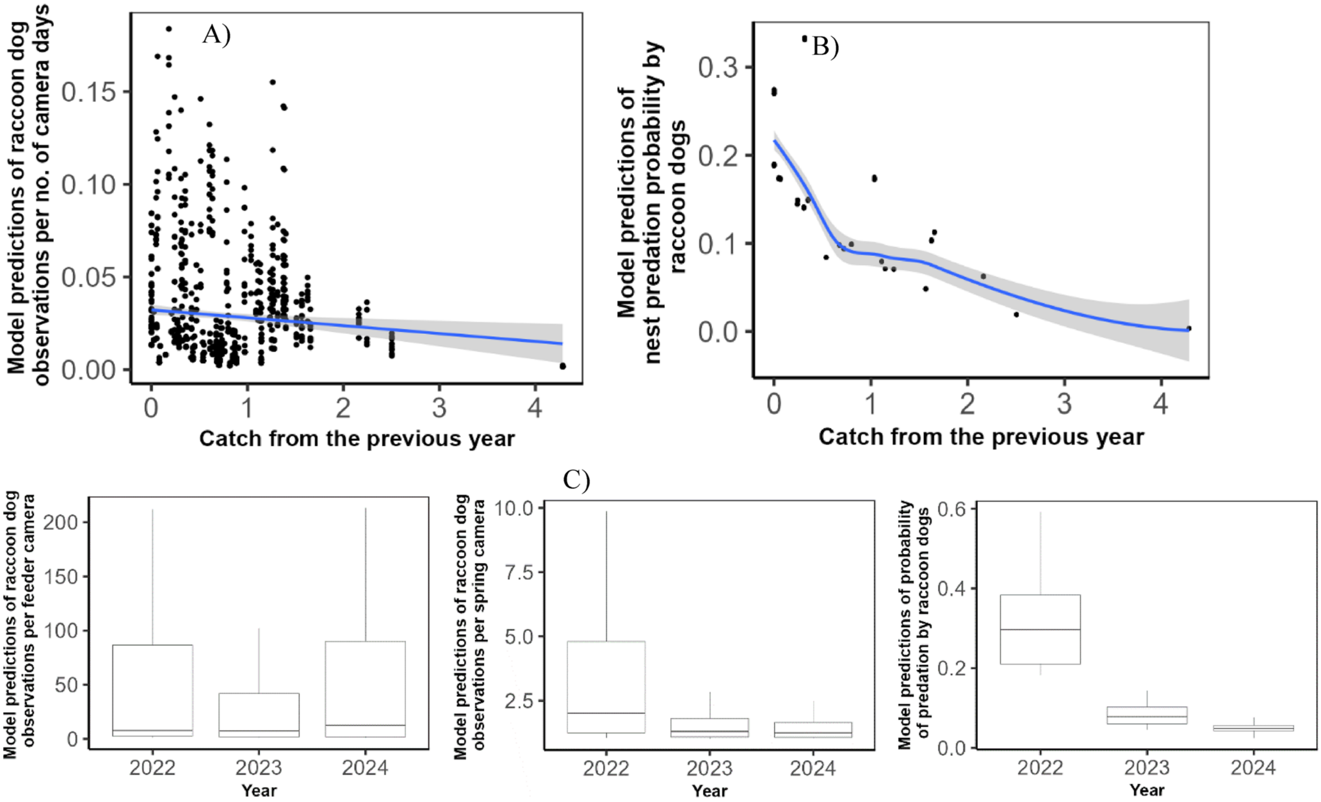

Fig. 3 Effect of catch of raccoon dogs in the previous year (average per month and per 1000 ha) on raccoon dog wildlife camera observations and artificial nest predation. (**A**) Spring camera observations ($n=31$ wetlands; zero catch values are from year 2021); (**B**) predation of artificial nests ($n=12$ wetlands). Points are predicted values and the line predicted trend. (**C**) Interannual changes in feeder camera (mainly winter) and spring camera observations and artificial nest predation level near wetlands important for waterfowl conservation

Table 4 (**A**) Factors affecting predation of artificial duck nests by raccoon dogs in along 12 wetlands (random effect) during 2022–2024 (n = 257 nest trials) modelled using binomial error distribution. (**B**) Yearly changes in nest predation by raccoon dogs and other predator species with post hoc comparisons using the contrasts command of the emmeans package (see methods for analysis of yearly changes).

(A)	Estimate	SE	*Z*-value	*p*-value
Intercept	–0.63	8.99	–0.07	0.94
Catch previous year	**–1.02**	**0.47**	**–2.18**	**0.02**
Catch current year (Feb–May)	0.007	0.01	0.69	0.49
Length of growing season	–0.006	0.05	–0.12	0.90
Length of observation period	0.04	0.12	0.33	0.74
(B) Contrast				
All predation				
2023 – 2022	**–2.09**	**0.47**	**–4.44**	**< 0.001**
2024 – 2023	0.23	0.23	0.671	0.75
Raccoon dog alone				
2023 – 2022	**–1.60**	**0.56**	**–2.86**	**0.008**
2024 – 2023	–0.65	0.58	–1.12	0.43
All other than raccoon dogs				
2023 – 2022	–0.81	0.45	–1.80	0.12
2024 – 2023	0.56	0.42	1.31	0.30
Corvids alone				
2023 – 2022	–0.30	0.43	–0.70	0.69
2024 – 2023	0.16	0.39	0.42	0.87

Variables with significant p-value are in bold.

Our study did not identify a definitive threshold for minimum effort required for successful raccoon dog control. Increase in cumulative control effort decreased monthly catches, indicating diminishing returns, but determining a precise threshold below which reduced effort compromises program effectiveness proved challenging and likely varies regionally. Consistent with previous research (Lazure and Weladji 2024), we found differential effectiveness among hunting methods. Proportion of time used for den hunting exhibited strongest positive relationship with total catch. We did not detect significant differences between other methods, but stand hunting exhibited marginally significant negative effect on total catch. It is important to note that our comparison was based solely on time invested and total catch, but by using the proportion of time used for each catch we could analyze how their relative use influenced the total catch. Negative effect here indicates that in relation to other methods stand hunting appeared less effective in explaining the total catch. From the used methods, den hunting is effective once the active nests have been located and it often succeeds in removing individuals prior to breeding. Individuals need to be excavated, but the use of trained dogs to chase the raccoon dogs from the den increase efficiency.

Similarly, hunting dogs played a crucial role in the effectiveness of baying dog hunting by facilitating raccoon dog detection. Trapping is known to have the problems related to trap shyness of individuals that decreases trapping success. The trapped individuals may also be biased towards young unexperienced individuals with a low contribution to population size compared to adult individuals (e.g. Escobar-González et al. 2024).

In their review, Bengsen et al. (2020) concluded that shooting can be an effective management tool, although many studies have failed to demonstrate a significant population impact. These failures are often attributed to insufficient population reduction. For example, in Australia, shooting was previously considered ineffective, but more coordinated programs have shown improved outcomes (McLeod et al. 2011). Modern shooting programs can further benefit from advanced technologies such as use of wildlife cameras and GPS with hunting dogs. However, much of the data on shooting effectiveness comes from studies on species other than mesopredators, such as deer and wild boar (Bengsen et al. 2020). The existing mesopredator studies, mainly on red fox, report mixed results, although shooting has successfully eradicated cats from islands (Bengsen et al. 2020). Our findings support the conclusion that coordinated shooting programs that combine different methods can be effective (Newsome et al. 2014), but complete eradication likely requires sustained effort over multiple years, with sufficiently high annual hunting pressure. Size of the hunting area will influence the catch, while excessively small hunting areas can be vulnerable to immigration from surrounding areas (e.g., Hanson et al. 2009; Lieury et al. 2015), overly large areas can hinder concentrated efforts in critical conservation zones (Simard et al. 2013). A targeted hunting approach focused specifically on prey breeding habitat before their breeding season might improve control effectiveness. Such a targeted approach could also enhance social acceptance of lethal control methods by increasing selectivity (Swan et al. 2017).

Evaluating the effectiveness of a control program requires assessing both predator removal rates and impacts on protected targets (Smith et al. 2010; Lennox et al. 2018; Treves et al. 2019; Lazure and Weladji 2024). In our case, raccoon dog abundance, as indicated by camera trap observations, presented mixed results. Camera-trap data from feeding sites at winter did not reveal a clear local decline in raccoon dog presence over time or in relation to catch in previous year. One possible explanation is substantial immigration from areas outside the hunting zone, masking the effects of local removals. Juvenile raccoon dogs mainly disperse in autumn (Sutor 2008; Drygala et al. 2010) and adults in both autumn and early spring (Herfindal et al. 2016). If autumn immigration filled the eradicated raccoon dog territories, we would expect current-year hunting to have a more pronounced effect on spring camera-trap observations compared to previous years' hunting. The absence of such an effect is curious, but likely related to our inability to control density (see below). Removal of more raccoon dogs in spring might also open up more territory space to be filled by immigrants that might increase movement in front of cameras. Alternatively, the used method for data gathering during winter prevented observing slight winter decline at feeding sites. That is, for feeder cameras hunters may sometimes have strategically relocated cameras during the survey to optimize hunting success. However, these cases did not appear very common (see methods). The feeder camera data shows that raccoon dogs were present in the areas in winter despite the control program, but the data may have been unsuitable in detecting slight declines in the raccoon dog numbers. Furthermore, broader trends, as indicated by Finnish snow-track data, suggest a potential increase in raccoon dog populations between 2023 and 2024 (Natural Resources Institute Finland 2024), which could have influenced our local results. However, interpreting snow-track data without accounting for temperature is problematic for raccoon dogs (Selonen et al. 2024b), necessitating caution when extrapolating these broader trends to our study.

In spring, camera traps placed around wetlands showed a decline in raccoon dog observations over time and in relation to catch in previous year. This decline was most pronounced in the first year of the study, slowing thereafter. However, complete eradication was not achieved at any site based on feeder camera data, although in few cases zero observation were made in spring cameras. While the timing of removals is generally critical for management efficacy (Conner et al. 2015), our data indicated that only previous year catch had a detectable impact. We found a positive, albeit weak, relationship between current-year hunting (before spring) and raccoon dog spring observations, suggesting that high hunting success simply reflected high local raccoon dog abundance, possibly due to strong immigration. This observation could also be influenced by the suspected regional population increase between 2023 and 2024 in snow-track data (Natural Resources Institute Finland 2024). Furthermore, localized factors, such as the proximity of hunting to wetlands, may have played a role. Additionally, in many sites, hunting efforts failed to remove mated pairs, a critical factor given the raccoon dog's monogamous nature. Our previous research (Toivonen et al. 2025) suggests that management strategies that result in solitary individuals can lead to increased wandering and subsequent influx into wetland areas. Of the methods employed, only den hunting effectively removed mated pairs. Consequently, management strategies that produce solitary individuals with increased movement activity may have diminished the impact of current-year control efforts on subsequent camera-trap observations. Future management should consider these factors to optimize hunting strategies.

Raccoon dogs, along with crows, were the primary predators of artificial nests in our study, which is consistent with previous findings in Finland (Holopainen et al. 2021, 2024). Increased catch in the previous year was associated with a clear decrease in raccoon dog nest predation. This relationship appeared stronger, compared to that in analysis of raccoon dog abundance, perhaps because the sites with artificial nests were mainly in southern Finland with high raccoon dog density. These higher densities may have increased hunter motivation and catch probability (see, e.g., McDonald et al. 2007; Williams et al. 2013) compared to northern regions with lower raccoon dog densities. Importantly, the observed decline in raccoon dog nest predation did not lead to a compensatory increase in predation by other species. Consequently, the raccoon dog control program appears to have effectively reduced overall nest predation pressure within our study sites (see also Tapper 1996; Fletcher et al. 2010; Roos et al. 2018). While acknowledging that artificial nest predation may not perfectly reflect predation rates on natural nests, particularly those of declining bird species, our data suggest a link between reduced raccoon dog abundance near wetlands and a potential positive impact on the breeding success of associated prey species.

We conclude that a coordinated control program can reduce raccoon dog numbers and benefit wetland bird species (here indicated by reduced predation on artificial nests). Our findings are consistent with previous research on restricted-area culls of red foxes, which indicate that while culling can temporarily reduce local abundance, sustained reductions require continuous removals due to rapid immigration (Baker and Harris 2006; Newsome et al. 2014; Lieury et al. 2015; Porteus et al. 2019). We observed a clear decline in raccoon dog presence and a corresponding reduction in artificial nest predation during the spring breeding season, but no significant decline in winter feeder camera observations. Thus, complete eradication proved difficult, and a relatively rapid return to pre-control population levels is probable, despite the substantial effort (on average 0.6 person-years of work per wetland each year) put into the control measures. That is, without substantial effort and continued predator removal, any positive effects on prey populations will likely be short-lived due to subsequent predator immigration (Duebbert and Lokemoen 1980; Tapper et al. 1982; Minnie et al. 2016; Lennox et al. 2018). However, careful consideration of factors such as hunting method effectiveness and the spatial scale of management likely will increase the success of the program. Future studies are needed to evaluate the effects of predator control or eradication on endangered bird populations, and its effectiveness in relation to other management and restoration actions that aim to improve wetland conservation.

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Author contributions TL and VS conceived the idea. KK, MT, PD and VS contributed in data collection. PD, AL and VS analyzed the data and produced figures. VS led the writing of the manuscript, and all the authors gave final approval for the publication.

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Data availability The data for numbers of hunted raccoon dogs and hunting hours are available in the supplement, but other datasets analysed during the study are on large part owned by Finnish wildlife agency that are not publicly available but are available from the corresponding author on reasonable request.

Declarations

Ethical approval Ethics approval was not required for this study.

Competing interests The authors declare no competing interests.

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