

Protecting prey by deceiving predators: A field experiment testing chemical camouflage and conditioned food aversion

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ABSTRACT

Complicated conservation problems may arise if predator numbers increase beyond their natural boundaries due to anthropogenic influence. For example, dramatic declines in ground-nesting birds are linked to increased nest predation by alien or human-subsidized mammals. While predator control can be temporarily effective, it is often laborious and carries ethical issues. Thus, we need alternative, non-lethal methods for reducing predator impact on their prey. We performed a landscape-scale experiment to study whether two non-lethal methods could protect ground-nesting waterfowl from nests predation. We spread either non-rewarding waterfowl odour (chemical camouflage) or eggs containing an aversive agent (conditioned food aversion) in the surroundings of study wetlands located in southern Finland. Predation of artificial waterfowl nests by red foxes decreased in sites with chemical camouflage, while there was no effect on predation by invasive raccoon dogs. Food aversion created less obvious effects than the chemical camouflage, but both methods indicated potential for reducing nest predation. Based on wildlife-camera data mesopredator observations did not, however, decrease near treatment wetlands. This suggests that treatments did not reduce predator activity, but affected foraging behaviour of predators and reduced their ability to find the nests. We conclude that managers considering non-lethal methods should carefully consider the effectiveness of different methods and potential species-specific responses. Nevertheless, our study support calls for wider use of non-lethal methods in reducing predator impacts on prey. These methods offer ethical and potentially effective approaches which keep native predator fauna intact, but create protection for vulnerable prey.

1. Introduction

Predators are important for the healthy function of natural ecosystems (Terborgh and Estes, 2010; Prugh and Sivy, 2020), but complicated conservation problems may arise if predator numbers increase beyond their natural boundaries due to anthropogenic influence (Estes et al., 2011; Smith et al., 2010). In particular, alien predators have caused the declines of numerous prey species' populations worldwide (Genovesi, 2005; Salo et al., 2007), and the numbers of native mesopredators have also increased in many human-dominated landscapes due to food subsidies and lack of apex predators controlling their numbers (Ritchie and Johnson, 2009; Wallach et al., 2015). A common intervention is to control the numbers of excess predators, alien or native, from the system (e.g. Reynolds and Tapper, 1996).

While removal of predators can be temporarily effective, it is often laborious and carries ethical issues regarding animal rights and welfare (Genovesi, 2005; Lennox et al., 2018). Lethal control is difficult to implement without causing collateral harm or disturbance to non-target species (Virgós et al., 2016). It may not be accepted by some stakeholders, and in some strictly protected areas, all hunting may be forbidden, even for conservation purposes (Genovesi, 2005). Ethically sound alternative approaches are therefore urgently needed to reduce predation pressure when it is essential to protect threatened prey species (Greggor et al., 2016; Norbury et al., 2021).

Two non-lethal methods for locally reducing predator impact on their prey include chemical camouflage (CC) and conditioned food aversion (CFA). CC involves spreading non-rewarding prey-like odour in the area to induce habituation of mammalian predators to there being no

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reward, or to make the cue useless for them via background matching effects (Price and Banks, 2012). Thus, the CC treatment prevents predators from using the odour as a cue or increases the effective search time for each food item gained, because time is wasted investigating unproductive cues (Carthey et al., 2011). This method has been successfully applied in reducing odour-based mammalian predation on artificial bird nests in Australia (Price and Banks, 2012) and on free living birds in New Zealand (Norbury et al., 2021). CFA again is a form of classical conditioning, in which predators consume food that makes them feel ill, leading them to learn to avoid this food (Snijders et al., 2021). CFA can be induced deliberately by adding a chemical substance to the food or prey desired to be protected from predation, in order to produce rejection by the predator (Nicolaus et al., 1989; Tobajas et al., 2021). The idea that CFA could be used to protect prey from predators is at least 50 years old (e.g., Gustavson et al., 1974), but only now we have reached a stage where field-safe methods that do not excessively harm the target animals (or other species in the environment) are becoming available (Tobajas et al., 2019, 2020a). Despite both CC and CFA showing great potential in reducing undesired predation of prey, we need more information on the relative usefulness and effectiveness of these two methods in reducing predator impacts in different systems with different predators if they are to be adopted widely.

One group of endangered prey, for which increasing predator populations appear to cause declines is ground-nesting birds (Dahl and Åhlén, 2019; Nummi et al., 2019; Koshev et al., 2020; McMahan et al., 2020; Pöysä and Linkola, 2021). For example, in Europe, the decline of ground-nesting birds appears a continent-wide phenomenon (McMahon et al., 2020). These species are preyed on by mammalian mesopredators and corvids that in many countries maintain high densities due to low numbers of top predators and human food subsidies in winter (Ritchie and Johnson, 2009; Tobajas et al., 2022). On top of native mesopredators, invasive species such as the raccoon dog (*Nyctereutes procyonoides*) in Europe, affect negatively nesting success of ground-nesting birds (Krüger et al., 2018; Dahl and Åhlén, 2019; Holopainen et al., 2020a, 2020b, 2021; Koshev et al., 2020; but see Kauhala and Kowalczyk, 2011). For example, waterfowl populations have declined dramatically in just a few decades in Finland, with some species declining as much as two-thirds or even 90 % since the late 1980's (Laaksonen et al., 2019). Thus, whether caused by invasive or native predators, attempts to reduce predation are clearly needed for reversing the population trends of waterfowl.

We performed a landscape-scale experiment to study whether CC (chemical camouflage) and/or CFA (conditioned food aversion) could protect waterfowl nests from predation in the boreal wetlands. We spread either (i) non-rewarding waterfowl odour (CC) or (ii) eggs containing a food-aversive agent (CFA) in the surroundings of wetlands, with control sites that were visited as frequently as the treatment sites for controlling a potential disturbance effect. We analysed whether these treatments affected a) mesopredator activity (as detected with wildlife cameras) or b) predation of artificial waterfowl nests in the post-treatment period. We predicted that the treatments would either 1) reduce the activity of the predators in treated areas because it has become less rewarding for foraging; and/or 2) reduce predation on artificial nests in treated areas because the predators stop predation or have difficulties in finding the nests.

2. Material and methods

2.1. Focus predators in the experiment

The main mesopredators in Finland include the raccoon dog, the red fox (*Vulpes vulpes*), and the Eurasian badger (*Meles meles*). The raccoon dog is an omnivorous canid predator that weighs typically 5–9 kg. It is the only invasive mesopredator in the country and invaded Finland from Soviet Union in the 1950s (Kauhala and Kowalczyk, 2011). The red fox is a native mesopredator in Finland, it weighs typically 5–8 kg and is

omnivorous, but is more carnivorous than the raccoon dog, preying more often on birds and mammals (Kauhala et al., 1998). The other native mesopredator, the badger, is also an omnivorous predator feeding e.g. on invertebrates, amphibians and small rodents (Kauhala et al., 1998). Its mean weight is from 9 to 12 kg (Macdonald and Barrett, 1993). All the three mesopredators are known to predate waterfowl nests (Holopainen et al., 2021). Corvids and some smaller predators, e.g. invasive American mink (*Neogale vison*) are also important nest predators in Finland (Holopainen et al., 2021), but their occurrence in the study areas could not be determined from our wildlife camera data. However, visits by any predators to artificial nests were recorded.

2.2. Study sites and wildlife cameras

Eighteen study sites located in southern and central Finland were used for the experiment (Fig. 1). These were the shore areas of small lakes, large ponds or distinct areas of lakes that were known to be important areas for wetland birds in southwest Finland. On average the size of the study sites, as measured as a distance of shore area, was 3.0 ± 1.7 km (Table 1). The nearest neighbour distance between the study wetlands was on average 14 ± 13 km (min 3 km, max 50 km inter-lake distance). In order to study the occurrence of the focal predators in the study areas, 163 wildlife camera traps (Uovision, Shenzhen, China) were used. The number of wildlife cameras set to determine predator activity varied depending on size of the site (3–16 per site, Table 1), with the aim that the whole wetland was surrounded with cameras 200–300 m from each other.

The wildlife cameras were set in shore forests and at the edge of shore area surrounding the wetland (10–100 m from the shore edge). Some of the waterfowl of the wetlands, such as mallards (*Anas platyrhynchos*), Eurasian teals (*Anas crecca*) and Eurasian wigeons (*Mareca penelope*) nest in these shore forests, while other species nest in the wetland where we could not place our cameras. The forests in these areas are dominated by managed coniferous and mixed forests, with Norway spruce (*Picea abies*), scots pine (*Pinus sylvestris*), birches (*Betula* sp.), aspen (*Populus tremula*), and alders (*Alnus* sp.) being the most abundant tree species. Agricultural areas covered about 30 % of the landscape in the study areas. Human settlements are sparse in these areas, including mainly summer cottages. Wildlife cameras were not set close to human settlements and they were always placed with a permission from the landowner.

We installed wildlife cameras in April–May 2021 before the main breeding season of waterfowl (Table 1). Cameras were removed at the end of May - beginning of June when most nests of waterfowl had already hatched. The set-up date varied because the study sites were spread over southern Finland (Fig. 1) where spring starts earlier in coastal southwest compared to inland northeast of the area (about a week or two). Thus, the first cameras were set up to most south-western study sites (Table 1). In addition, flooding delayed installing of the cameras in some sites. The experiment needed to stop in some sites before grass growth hampered visibility in camera view in the end of May. Thus, the length of study period varied between study sites, but this was considered in the analysis. The cameras were set to take videos or in some cases photos. For the purposes of this study, videos were treated as a single photo, and only consecutive images of the same species separated by 30 min were included in the data as independent events (that is, multiple photos within this time period were considered as the same event; O'Brien et al., 2003). Cameras were set-up to high sensitivity mode, and, thus, we assume that the cameras well detected the mesopredators moving in front of them. We did not use any attractants near the cameras.

2.3. Experimental set up

The experimental design consisted of six wetland sites that received CC, six that received CFA, and six that were left as untreated control

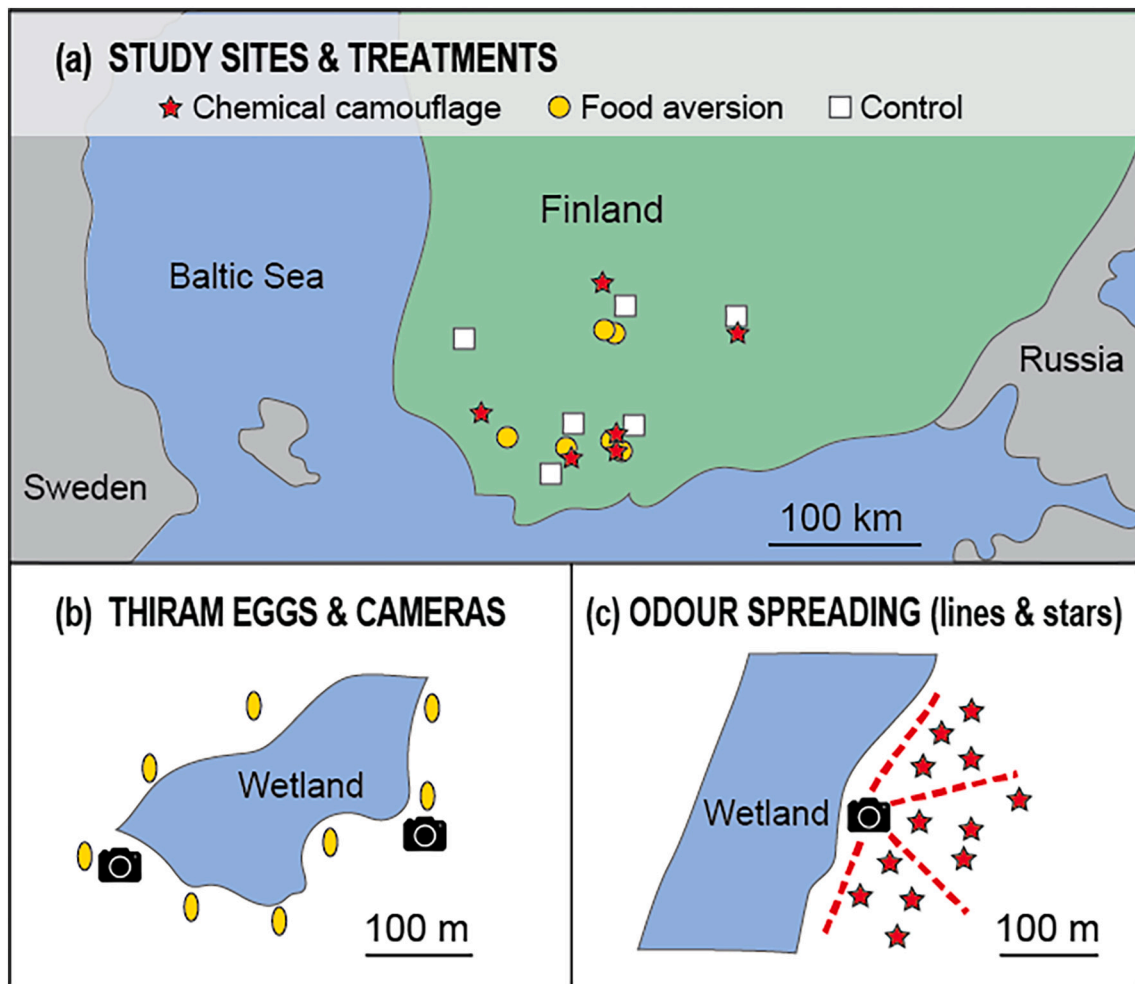


Fig. 1. The eighteen study sites with chemical camouflage treatment (CC, 6 stars), food aversion treatment (CFA, 6 circles) and control sites (6 squares) in southern Finland in spring 2021. In addition, examples of placing of thiram eggs (yellow ovals; lower left panel) and spreading of waterfowl odour (lines and stars; lower right panel) in relation to cameras during the five separate treatment visits to study sites. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Study sites and total number of mesopredator observations (the raccoon dog, the red fox, and the badger) during the on average 44 days study period in wildlife camera data in 18 wetlands in southern Finland.

Study site	Shore distance (km)	Raccoon dog	Red fox	Badger	No. of cameras	Installation day	Camera days	RAI ^a	Treatment
Koskeljärvi	3.7	11	35	1	10	04/16/2021	480	9.8	Control
Omenojärvi	5.1	47	20	1	15	03/31/2021	720	9.4	Control
Saarenjärvi	1.4	2	3	0	4	04/14/2021	152	3.3	Control
Saarioisjärvi	4.9	24	21	7	13	04/12/2021	481	10.8	Control
KutajärviN	4	46	0	4	11	04/07/2021	517	9.7	Control
Vanjärvi	3.8	21	20	25	10	04/14/2021	420	15.7	Control
Sum		151	99	38	63		2770		
Alhainen	0.9	11	1	22	3	04/12/2021	120	28.3	CFA
Härmälä	0.8	6	14	4	4	04/01/2021	184	13.0	CFA
Savijärvi	3.7	66	22	77	13	04/07/2021	624	26.4	CFA
Vaanila	4.5	83	10	21	13	04/06/2021	650	17.5	CFA
Vitikka	0.8	12	2	0	3	04/12/2021	135	10.4	CFA
Vuorela	0.9	13	13	0	4	04/04/2021	160	16.3	CFA
Sum		191	62	124	40		1873		
Kutsila	4.1	105	37	112	12	04/06/2021	552	46.0	CC
Kirkkojärvi	1.7	10	3	7	5	04/15/2021	165	12.1	CC
Koisjärvi	3.5	47	16	7	13	04/07/2021	637	11.0	CC
Ahtialajärvi	3.8	52	31	13	10	04/09/2021	420	22.9	CC
Järvelä	1.3	3	6	0	4	04/02/2021	188	4.8	CC
KutajärviS	6	33	22	4	16	04/09/2021	752	7.8	CC
Sum		250	115	143	60		2714		

CFA = conditioned food aversion (thiram eggs), CC = chemical camouflage (bird odour).

^a Relative Abundance Index (RAI, predator observations/100 camera days).

wetlands. The first treatment or control visit was made a week after the cameras were set-up in the study sites. Treatment and control had five separate visits to each study site with 5–7 days between visits. Thus, thiram treated eggs (see below) in the CFA and odour of waterfowl in the CC likely were always present in the sites during the treatment. During the visits to the study areas, we followed the routines for treatment and control visits outlined below and in Fig. 1.

2.3.1. The chemical camouflage (CC) treatment

To six study sites (Table 1) we spread a mixture of selected waterfowl odour products (see below). This was done to four directions from each wildlife camera up to 150 m from the camera: both directions along the shoreline from the camera and to two directions to inland, depending on the presence of fields and human settlements (Fig. 1). The odour substance was applied every 10 m along each line with either odour-treated sticks placed on the ground, or by scrubbing the odour to tree bases and stumps. In addition, the odour substance was spread between the lines randomly to points 30 m from each other (Fig. 1). For the bird odour substance, we used a mixture of duck grease (from a farmer), duck preen gland oil, and waterfowl odour product used in training of dogs (commercial product). In a previous experiment (Norbury et al., 2021) a mixture of several different bird odours was argued to be effective in predator habituation in protecting a multi-species bird assemblage.

2.3.2. The conditioned food aversion (CFA) treatment

In six other study sites (Table 1), we added domestic mallard or goose eggs containing 100 mg of thiram, which was injected to egg by removing the same amount of egg content in laboratory 1–2 days before taking the eggs to field (following guidelines described in Tobajas et al., 2020a). Thiram is a dithiocarbamate fungicide that has been successfully used as a repellent and is recommended to be used for CFA experiments (Tobajas et al., 2019, 2020a, 2020b). At the dose able to induce CFA, thiram causes digestive signs (vomiting, nausea and/or diarrhoea) without other severe adverse health effects (Tobajas et al., 2020b). The effect of thiram appears around 1 h after exposure (Tobajas et al., 2019, 2020b). To get a thiram dose needed for CFA the minimum dose is of 40–50 mg/kg body weight (Tobajas et al., 2019; Tobajas et al., 2020a, 2020b). In our case, this was achieved for an animal weighing 5 kg with two eaten eggs when one egg had 100 mg of thiram. The weight of both raccoon dogs and red foxes is at lowest in spring time in Finland, about 5 kg (Kauhala, 1996), but badgers likely weighed more than this (likely 5–10 kg at spring).

For each wildlife camera location, three to four eggs were placed 50–100 m from each other along the shoreline (Fig. 1). The shoreline is used for travel by animals moving in the region (own observations). The thiram eggs were placed in artificial nests mimicking waterfowl nests on the ground. The nests consisted of one egg treated with thiram as well as mallard or goose feathers that were treated with bird odours (the same product as for CC). The latter increased the likelihood for predators to locate the nests and the resemblance of the real situation where a bird is visiting or present at the nest. In total 520 thiram eggs were used, 42–165 per study site, depending on the number of cameras. Based on density estimates from the wildlife camera data, the mesopredator densities are low in these areas (1 /km² for raccoon dog and < 1 /km² for the red fox and the badger; V. Selonen, T Laaksonen, unpublished data). Thus, an individual moving along the shoreline likely encountered several eggs. Our approach allow the predators to eat several thiram eggs while the intake of treated eggs by non-target species is minimized, which should be a priority in non-lethal predation control experiments (Smith et al., 2022). Eggs eaten between the visits to the area were replaced with new thiram eggs until the end of the treatment (total treatment time on average 30 days). All non-eaten eggs were collected from the field in the end of experiment.

The remaining six study sites were untreated controls (Table 1). They were visited as often as the CC and CFA sites. During the visits we walked from the wildlife cameras, following the pattern similar to CC treatment

without spreading any CC or CFA products.

2.3.3. Post-treatment artificial nests to measure predation rates

After the last treatment visit, we placed artificial nests (intact eggs without thiram) in front of the wildlife cameras in each of the 18 study areas. The artificial nests were built from grass and mallard feathers treated with the same bird odour substance used in CC treatments, and included one mallard egg (in the end, eight cameras remained without an artificial nest, so the total $n = 155$ nests for this experiment, 56 for control, 40 for CFA and 59 for CC; depending on number of cameras in each wetland). The artificial nests were in a spot in front of camera, where we had not placed CC or CFA. After 6–8 days (i.e. on average the last week of the experiment) the status of eggs was checked (preyed on vs. not preyed on) and cameras were collected away from the field (the experiment ended). This period is shorter than a typical incubation period of focal waterfowl (typically three to four weeks), but gives an index of predation rate within the study sites that earlier has been shown to measure high predation rates (e.g. Holopainen et al., 2021). The predator species likely responsible for eating the egg was later checked from wildlife camera data. It should be noted that we could not estimate nest-predation rate before treatment. The reason for not using Before-After design is that the season when eggs are in nests is short in the area. In addition, placing artificial nests before experiment would have interfered with the application of the treatment, by increasing the supply of uncamouflaged and palatable eggs available to predators.

2.4. Analyses

2.4.1. Mesopredator activity in treatments and controls

- (1) To compare the number of mesopredator observations in the treatment and control areas, we built models with the dependent variable being either the number of all mesopredator observations or only the raccoon dog or red fox observations in a wildlife camera ($n = 163$) during the study period. We omitted the badger from species-specific analyses, because they caused less nest predation than red foxes and raccoon dogs. For each model, a negative binomial distribution was used. The explanatory variables included in the models were treatment (class variable: 1 = control, 2 = CFA, 3 = CC), habitat at the camera site (class variable: 1 = herb-rich forests and herb-rich heath forests, 2 = heath forests, 3 = edge of field and forest near the shore, 4 = semi-open meadows/bush area at the shore), and total days the camera was on (continuous variable). The study site was set as a random effect and Kenward-Roger approximation method was used for degrees of freedom in the Glimmix procedure of SAS 9.4. software.
- (2) To analyse whether the number of predator observations changed in time in treatment and control sites during the experiment, we divided the data to 5 time periods. A period was on average a week long, but varied because the total length of the survey period varied between cameras and study sites (see above and Table 1). We built Poisson models where the number of predator observations in a camera during each of the 5 time periods was the dependent variable (note that the daily probability of an observation was very low and could not be used as a dependent variable in this analysis). The same explanatory variables as above were used, except that time (continuous variable for the periods 1–5) and the interaction term between time and treatment were included in the model. This interaction term was used to analyse whether predator numbers changed differently in time between control and the two treatments. In addition, camera identity was included as random effect to account the repeated measures per camera. Three models were built, first for all

mesopredator observations, and then including only the observations of the raccoon dog or the red fox.

- (3) We tested whether the predation of thiram eggs changed in time in CFA sites (during the 5 treatment visits to the sites). We made an events/trial model where the event was the number of eggs observed to be preyed on at a visit to the site, and the trial was the total number of eggs in the study site set during the previous visit (eaten eggs were replaced with new thiram eggs during each visit). The running number of the visit (1–5) was set as the explanatory variable and study site as a random effect.

2.4.2. Post-treatment artificial nests

- (4) We analysed whether treatments affected predation rates by using the fate of artificial waterfowl nests at camera sites during post-treatment period (the last week of the experiment). We built a model with the dependent variable being the nest being preyed on or not (binomial model). Treatment (class variable: 1 = control, 2 = CFA, 3 = CC), habitat at the camera site (class variable described above), total number of mesopredators observations in the camera during the whole study period, and the number of days the artificial nest was in the field (6–8 days) were included as explanatory variables in the model. The study site was set as a random effect and Kenward-Roger degrees of freedom approximation was used in Glimmix procedure of SAS 9.4. We used a binomial model for nest predation instead of performing survival analysis, because it was in several cases not clear on which day the nest was preyed on.
- (5) In order to analyse whether there were differences between predators in response to the treatments, we performed an analysis where the above nest predation model was run separately (a) for the red fox, (b) for the raccoon dog (the two species mostly responsible for the predation), and (c) combining all other predators, including cases where the predator was unknown. In these models, the dependent variable was the artificial nest preyed on (by the red fox, by raccoon dog, or by “other”) vs. not preyed on (binomial model). The model was similar as above (4), except that we included also a two-class explanatory variable whether the nest was preyed on or not by other predators than the one in the dependent variable. This was done to control for the effect of predation by other species than the one being in the focus of the analyses (Tobajas et al., 2020a).

In all above models, spatial correlations in the residuals were accounted for by adding coordinates of cameras as a random effect in the model, except in the model (2) for effect of time on predator observations where camera identity was set as random effect. The effect of the size of study site was tested in each model, but it had no effect and was dropped from final models. LSmeans statement in SAS Glimmix was used to produce estimated marginal means and pairwise comparisons for explanatory class variables in the model (treatment or habitat variables).

3. Results

In total we recorded 1173 mesopredator observations with 163 cameras during an on average 44-day study period. The raccoon dog was the most frequently observed predator, being observed twice as often as the red fox or badger (Table 1).

3.1. Mesopredator activity in treatments and controls and consumption of thiram eggs

The number of all mesopredator observations or that of raccoon dog/

red fox did not differ among treatments and control (Table 2). The number of all mesopredator observations did not change differently during the experiment in treatment or control sites (Table 3a; Fig. 2). However, when the invasive raccoon dog was analysed alone, there was a slight time effect (significant time period^atreatment interaction in the model, Table 3b), due to slight decreases of observations in control and CC sites, which did not appear to happen in CFA sites (Fig. 2). For the red fox we did not make the same observation, but the red fox observations increased in time during the experiment (Table 3c, Fig. 2).

In the CFA sites, on average $58 \pm 25\%$ of thiram eggs had been preyed on between each visit to the sites. The proportion of thiram eggs preyed on declined in time (estimate -0.63 ± 0.13 , $F_{1,18.2} = 21.2$, $p < 0.001$). Based on model predictions the decrease was from $85 \pm 7\%$ to $36 \pm 13\%$ of thiram eggs being preyed on in the first week and in the of last week of the treatment, respectively.

3.2. The post treatment artificial nests

The artificial nests ($n = 155$) set in front of wildlife cameras after the last treatment were less often preyed on in sites with CC treatment than in control sites (Fig. 3, Table 4). The response to CFA treatment seemed similar as that for the CC (Fig. 3), but the difference between control and CFA was marginally non-significant (Table 4). The red fox appeared to be the main driver of the observed CC treatment effect. That is, the effect of CC was significant only for the red fox (Fig. 3, Table 5a) and not for the predation by raccoon dogs (Fig. 3, Table 5b) or for the combined predation events by other predator species and unknown predators (Table 5c).

The red fox was most often identified to be the likely predator of the post treatment artificial nests (27 observations), followed by raccoon dog (22), badger (9), and corvids (8). In addition, pine marten and American mink were identified once, common crane twice and cervid two times to predate the artificial nests. In the rest 12 of the cases (out of 84 destroyed nests), the predator of the nest was unclear.

Table 2

Results of a Generalized linear mixed models (negative binomial) examining factors behind number of observations of a) all mesopredators, b) raccoon dogs, and c) red foxes in wildlife cameras ($n = 163$ cameras).

Effect	Estimate	F _{df}	p
a) All predators	Intercept = -0.20 ± 0.81		
Treatment (control, CFA, CC)	-0.4 ± 0.25 , 0.19 ± 0.28 , 0	2.2 _{2,15.8}	0.10
Habitat (1,2,3,4) ^a	0.09 ± 0.21 , -0.58 ± 0.28 , -0.07 ± 0.31 , 0	2.3 _{3,150.4}	0.08
Days camera on	0.03 ± 0.01	6.59 _{1,118.7}	0.01 ^c
b) Raccoon dog	Intercept = -0.89 ± 0.74		
Treatment (control, CFA, CC)	-0.4 ± 0.25 , 0.19 ± 0.28 , 0	1.93 _{2,16.9}	0.18
Habitat (1,2,3,4) ^a	0.09 ± 0.21 , -0.58 ± 0.28 , -0.07 ± 0.31 , 0	2.75 _{3,154}	0.04 ^b
Days camera on	0.03 ± 0.01	8.73 _{1,150.7}	0.003 ^c
c) Red fox	Intercept = -1.17 ± 0.94		
Treatment (control, CFA, CC)	-0.32 ± 0.52 , -0.27 ± 0.54 , 0	0.22 _{2,12.2}	0.81
Habitat (1,2,3,4) ^a	-0.19 ± 0.25 , -0.63 ± 0.34 , 0.29 ± 0.36 , 0	1.78 _{3,154}	0.15
Days camera on	0.04 ± 0.019	4.63 _{1,154}	0.03 ^c

CFA = conditioned food aversion (thiram eggs), CC = chemical camouflage (bird odour).

^a 1 = herb-rich forests and herb-rich heath forests; 2 = heath forests; 3 = edge of field and forest near the shore; 4 = semi open meadows/bush area at the shore.

^b In pairwise comparison difference between 1 (estimate 1.3 ± 0.15) and 2 (0.5 ± 0.26) $p < 0.05$, other not significant.

^c $p < 0.05$.

Table 3

Results of a Generalized linear mixed models (negative binomial) examining factors behind number of observations. a) Change in mesopredator observations in time (Poisson; total length divided to 5 periods, see main text), b) the same for only raccoon dog and c) red fox observations. $n = 140$ cameras for a) $n = 120$ for b) and $n = 102$ for c), that is, cameras without mesopredator observations omitted.

Effect	Estimate	F _{df}	p
a) All predators in time^a	Intercept = -0.51 ± 0.62		
Treatment (control, CFA, CC)	$-0.53 \pm 0.33, 0.14 \pm 0.34, 0$	0.78 _{2,9,1}	0.14
Habitat (1,2,3,4)	$0.16 \pm 0.17, -0.42 \pm 0.24, 0.14 \pm 0.26, 0$	2.23 _{3,138,5}	0.08
Time (periods 1–5)	-0.025 ± 0.03	1.59 _{1,672}	0.21
Time*treatment (control, CFA, CC)	$0.08 \pm 0.05, 0.07 \pm 0.05, 0$	1.70 _{2,672}	0.18
Days camera on	0.016 ± 0.012	1.70 _{1,114,8}	0.19
b) Raccoon dog in time	Intercept = -0.79 ± 0.64		
Treatment (control, CFA, CC)	$-0.26 \pm 0.31, -0.29 \pm 0.31, 0$	0.56 _{2,37,6}	0.57
Habitat (1,2,3,4)	$0.22 \pm 0.18, -0.45 \pm 0.26, 0.18 \pm 0.26, 0$	2.48 _{3,127}	0.06
Time (periods 1–5)	-0.14 ± 0.05	3.7 _{1,568}	0.06
Time*treatment (control, CFA, CC)	$0.06 \pm 0.07, 0.19 \pm 0.07, 0$	4.25 _{2,568}	0.02 ^b
Days camera on	0.02 ± 0.013	2.56 _{1,74,5}	0.11
c) Red fox in time	Intercept = -1.78 ± 0.74		
Treatment (control, CFA, CC)	$-0.03 \pm 0.41, 0.01 \pm 0.46, 0$	0.01 _{2,74,8}	0.99
Habitat (1,2,3,4)	$-0.05 \pm 0.21, -0.24 \pm 0.29, 0.03 \pm 0.29, 0$	0.27 _{3,126,4}	0.84
Time (periods 1–5)	0.14 ± 0.07	8.30 _{1,479}	0.004 ^b
Time*treatment (control, CFA, CC)	$0.02 \pm 0.09, -0.04 \pm 0.11, 0$	0.15 _{2,479}	0.86
Days camera on	0.016 ± 0.014	1.29 _{1,111,9}	0.26

CFA = conditioned food aversion (thiram eggs), CC = chemical camouflage (bird odour). Habitat variable, see Table 2.

^a Before start of treatment (first week of experiment) there were no difference in mesopredator observations per camera in CFA, CC and control sites (average \pm SD; control: 1.3 ± 2.1 ; CFA: 1.6 ± 1.4 ; CC: 1.9 ± 2.0 ; F_{df} = $0.7, 12, 4$, $p = 0.52$).

^b $p < 0.05$.

4. Discussion

The mesopredator observations near the wetlands did not decrease with our chemical camouflage (CC) and conditioned food aversion (CFA) treatments. Despite this, predation of artificial nests decreased, especially that by red foxes in CC sites (over tenfold decrease compared to control). For the predation by the invasive raccoon dog, we found no effect of either treatment. These results suggest mesopredators did not move away from treated study sites, but at least red foxes either had difficulties in locating the artificial nests or stopped foraging for them in sites with CC.

Our results suggest that the response to CC and likely also to CFA (see also Tobajas et al., 2020a, 2021) is species-specific. In our case, unfortunately the invasive raccoon dog was unaffected by our treatments. The raccoon dog is currently the most abundant mesopredator in Finland (Selonen et al., 2022) where it is equally important nest predator in wetland areas as the red fox (Holopainen et al., 2021). Why red foxes responded to the treatment while raccoon dogs did not remain unclear, but this likely relates to feeding behaviour of these species. Tobajas et al. (2020a) also found that red foxes developed conditioned food aversion towards bird eggs, while mustelids did not (see also Norbury et al., 2005; Tobajas et al., 2021). Thus, the red fox might be easier to deter from preying bird nests than some other mesopredators (see also Andrewartha et al., 2021). Red foxes are important predators of bird nests in many regions (Mateo-Moriones et al., 2012; Carpio et al., 2016), and may have increased in numbers above natural boundaries in large parts of Europe due to small numbers of apex predators (Terborgh and Estes, 2010). It is also an invasive species e.g. in Australia, where it creates

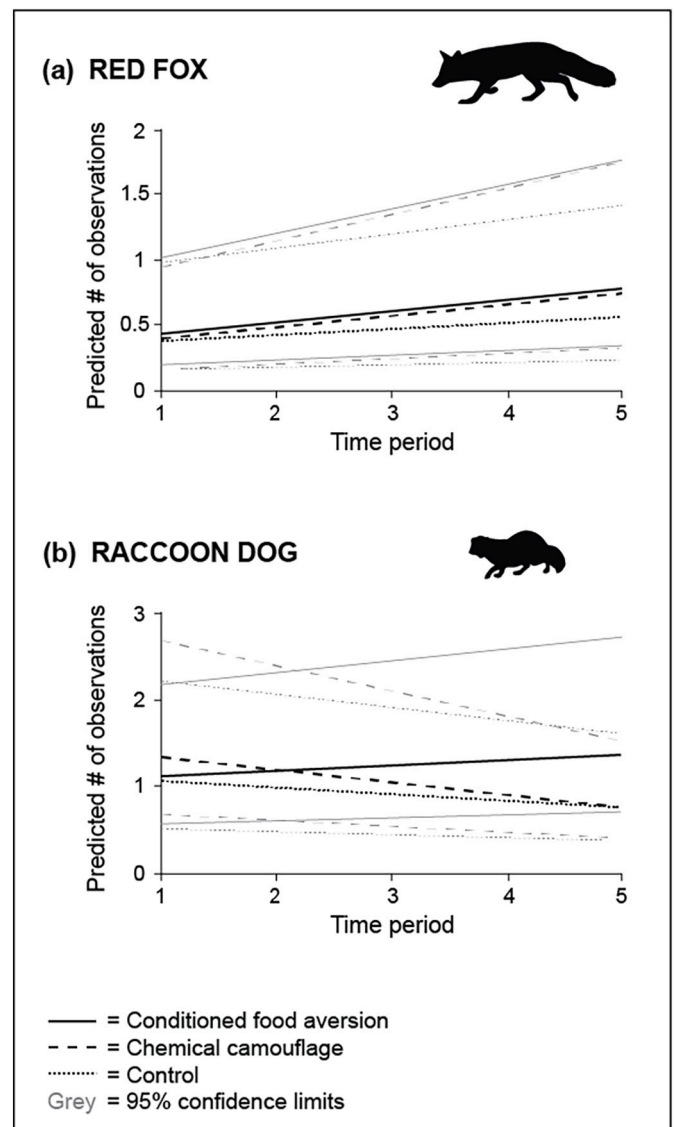


Fig. 2. The model predicted number of a) the red fox, and b) the raccoon dog observations in wildlife cameras during the five time periods of the experiment: 1 = on average the first week, ... 5 on average the last week of the experiment (total length 44 days on average; the total length varied between study sites, see main text). Short dashed line is the six control sites ($n = 63$ cameras), long dashed line is the six chemical camouflage sites (CC; $n = 60$ cameras), and solid line is the six conditioned food aversion sites (CFA; $n = 40$ cameras). 95 % confidence limits in gray. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

severe problems for native fauna (Wallach et al., 2010). Indeed, in many earlier studies, the red fox has been the focus mesopredator, the impact of which on local prey species has been the aim of reduction efforts (e.g. Wallach et al., 2015; Tobajas et al., 2021).

Our treatments can be seen as a training of predators on avoiding waterfowl nests, which is found to be an effective method for reducing predator impact on prey (Price and Banks, 2012). However, in our case for CC it is possible that there was odour present in the area even after the treatment stopped. That is, the intensive odour spreading may have caused camouflage effect still during post-treatment period, when artificial nests were in the area. This could cause red foxes not being able to use olfactory cues effectively when a large area had abundant odour of birds. Rains do occur in the area that will dilute the odour, but we are unable to evaluate how fast the odour disappeared from the ground. For the CC sites, the activity of the mesopredators in the area did not seem to

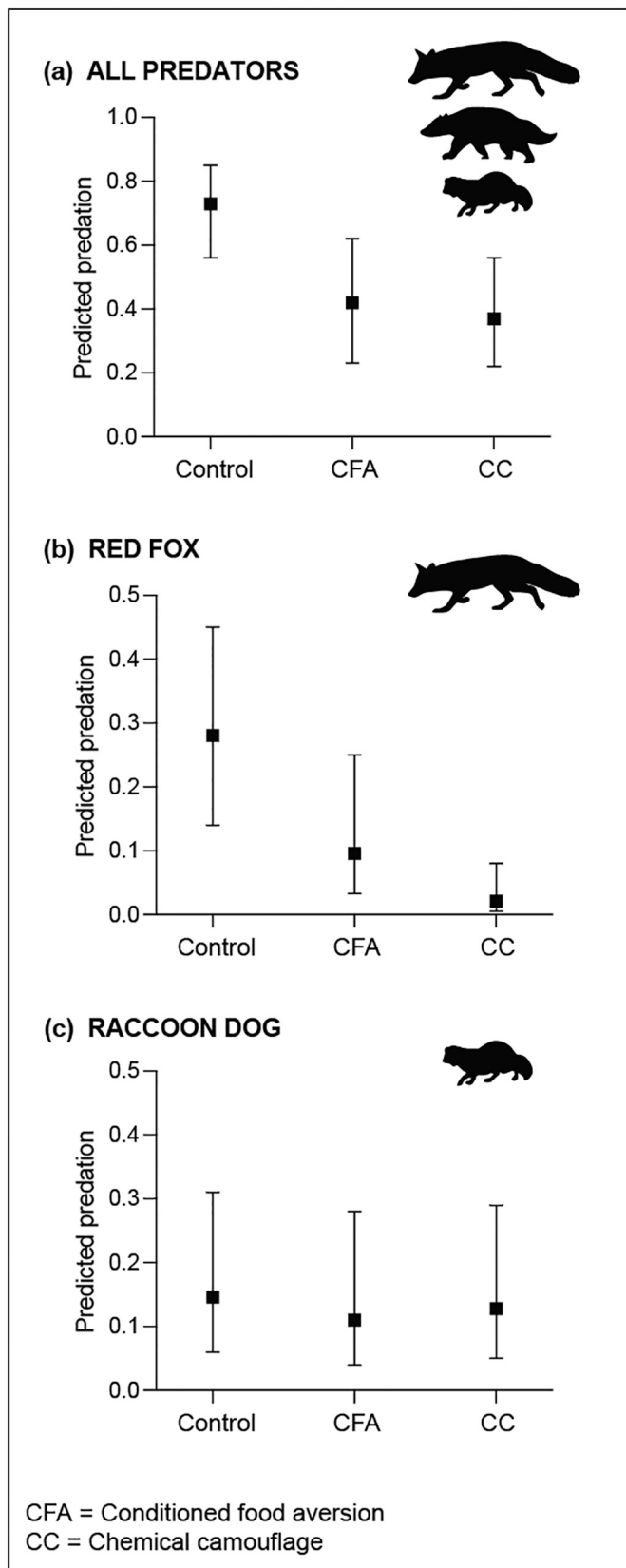


Fig. 3. The model predicted proportion (0–1, mean and 95 % confidence limits) of artificial nests preyed on in control sites ($n = 56$, average $n (\pm SD)$ for study sites: 9.3 ± 3.0), conditioned food aversion sites (CFA; $n = 40$, for sites: 6.7 ± 4.9) and chemical camouflage sites (CC; $n = 59$, for sites: 9.8 ± 4.4).

Table 4

Results of a Generalized linear mixed model (binomial) examining factors causing non-treated artificial nests being preyed on during post-treatment week of the experiment ($n = 155$ nests in 18 study sites).

Effect	Estimate	F _{df}	p
Intercept	-2.42 ± 1.99		
Treatment (control, CFA, CC) ^a	$1.51 \pm 0.46, 0.15 \pm 0.49, 0$	$5.9_{2,10.9}$	0.02^b
Total predators	0.08 ± 0.03	$6.7_{1,141.3}$	0.01^b
Habitat (1,2,3,4)	$0.33 \pm 0.44, -0.80 \pm 0.63, 0.28 \pm 0.65, 0$	$1.24_{3,128.6}$	0.29
Days nest followed	0.15 ± 0.25	$0.39_{1,30.2}$	0.54
Pairwise treatment effects		t _{df}	Adjusted p
Control vs CFA	1.27 ± 0.52	$2.6_{1,4.2}$	0.06
Control vs CC	1.45 ± 0.46	$3.27_{10.3}$	0.02^b
CFA vs CC	0.19 ± 0.50	$0.31_{9.8}$	0.95

^a CFA = conditioned food aversion (thiram eggs), CC = chemical camouflage (bird odour). Habitat variable, see Table 2.

^b $p < 0.05$.

Table 5

Results of a Generalized linear mixed model (binomial) examining factors causing non-treated artificial nests being preyed on a) by the red fox, b) by the raccoon dog, and c) by all other predators or unknown reasons ($n = 155$ nests in 18 study sites).

Effect	Estimate	F _{df}	p
a) Red fox	Intercept = -5.1 ± 2.1		
Treatment (control, CFA, CC)	$2.90 \pm 0.73, 1.61 \pm 0.78, 0$	$9.0_{2,13.6}$	0.004
Red foxes in camera	0.47 ± 0.10	$19.9_{1,100.6}$	0.0001
Habitat (1,2,3,4)	$0.30 \pm 0.57, -1.2 \pm 0.87, -1.19 \pm 0.90, 0$	$1.79_{3,94.3}$	0.15
Preyed on by raccoon dog or other (0,1) ^a	$-0.32 \pm 0.49, 0$	$0.49_{1,114.5}$	0.48
Days nest followed	0.08 ± 0.45	$0.03_{1,60.7}$	0.86
Pairwise treatment effects		t _{df}	Adjusted p
Control vs CFA	1.28 ± 0.59	$2.17_{10.2}$	0.13
Control vs CC	2.9 ± 0.72	$3.95_{22.7}$	0.002
CFA vs CC	1.62 ± 0.78	$2.04_{25.7}$	0.12
b) Raccoon dog	Intercept = -4.17 ± 3.8		
Treatment (control, CFA, CC)	$0.15 \pm 0.60, -0.19 \pm 0.66, 0$	$0.12_{2,10.5}$	0.88
Raccoon dogs in camera	0.15 ± 0.04	$11.5_{1,137}$	0.001
Habitat (1,2,3,4)	$0.13 \pm 0.57, -0.09 \pm 0.86, -0.07 \pm 0.86, 0$	$0.04_{3,132.9}$	0.99
Preyed on by red fox or other (0,1) ^a	$-0.67 \pm 0.49, 0$	$2.1_{1,146}$	0.15
Days nest followed	0.27 ± 0.49	$0.31_{1,52.6}$	0.58
Pairwise treatment effects		t _{df}	Adjusted p
Control vs CFA	0.35 ± 0.67	$0.48_{12.1}$	0.88
Control vs CC	0.15 ± 0.60	$0.28_{9.6}$	0.96
CFA vs CC	-0.19 ± 0.66	$-0.23_{10.3}$	0.97
c) Other or unknown	Intercept = -6.7 ± 3.9		
Treatment (control, CFA, CC)	$0.43 \pm 0.72, 1.0 \pm 0.76, 0$	$0.83_{2,8.3}$	0.46
Habitat (1,2,3,4)	$0.4 \pm 0.49, 0.51 \pm 0.64, 0.74 \pm 0.65, 0$	$0.51_{3,145.2}$	0.67
Preyed on by red fox or raccoon dog (0,1) ^a	$0.06 \pm 0.40, 0$	$0.02_{3,140.8}$	0.89
Days nest followed	0.68 ± 0.50	$1.86_{1,41.9}$	0.20
Pairwise treatment effects		t _{df}	Adjusted p
Control vs CFA	-0.57 ± 0.74	$-0.77_{8.9}$	0.73
Control vs CC	0.44 ± 0.72	$0.61_{8.0}$	0.82
CFA vs CC	1.01 ± 0.77	$1.30_{8.8}$	0.43

^a 0 = not preyed on, 1 = preyed on. CFA = conditioned food aversion (thiram eggs), CC = chemical camouflage (bird odour). Habitat variable, see Table 2.

be affected. That is, the treatment did not appear to increase mesopredator activity at the camera view (note that the odour spreading did not concentrate near the camera, but as far as 150 m from the camera). Instead, the thiram eggs (which were in artificial nests treated with bird odour) seemed to attract some raccoon dogs near to our cameras in CFA sites. In any case, that predators did not move away from the treatment area can be seen as positive, as the native predator fauna may remain intact by the treatment, which still may create protection for nests of waterfowl. Similar observations have been done in previous CFA (Tobajas et al., 2020a, 2021) and CC studies (Norbury et al., 2021) with red foxes. If predators maintain their territories despite the CC or CFA they could also expel immigrant conspecifics (Cowan et al., 2020; Norbury et al., 2021), which could prevent the density-dependent compensation caused by immigrants replacing the extracted individuals. This kind of negative effect is common in lethal predator control (Newsome et al., 2014; Porteus et al., 2018).

The CFA treatment created a less clear effect than the CC in our study. However, the effect seemed quite similar for both treatments (Fig. 3 all mesopredators). We had fewer artificial nests in the CFA than in the CC sites. The reason for this was that CFA sites were smaller than CC sites, because we had difficulties in producing large numbers of thiram eggs to be distributed over very large areas. This resulted in larger confidence limits for CFA than for CC in our analysis. In addition, we inserted 100 mg of thiram to each egg (following Tobajas et al., 2020a) with an expectation that an individual predator will encounter and eat more than one egg, which was required for the aversion effect (in our case 2 eggs, Tobajas et al., 2020a, 2020b; for 5 kg red fox or raccoon dog; Kauhala, 1996). The eggs were placed along the shoreline which is used for travel by animals moving in the area (pers. observation). The density of mammalian nest predators is low within our study area (see methods) and the nest predation by corvids remained at a low level in our study. Thus, an individual predator moving along the shoreline likely encountered several eggs in short time period and should have eaten more than one egg, because the predation rate of thiram eggs was high. We also used bird odour as attractant to increase encounter rate of nests with thiram eggs. In any case, we cannot be certain how many thiram eggs were eaten per individual, which ultimately would have been needed to be certain of effectiveness of CFA treatment.

Thiram has high toxicological safety margins (Tobajas et al., 2019; Tobajas et al., 2020a), but we sought to minimize the risk of ingestion of high doses of thiram and used conservative designs in favour of animal safety and welfare which should be a priority in studies with wildlife (Smith et al., 2022). In this regard, CC approach provides an advantage by not using chemical substances, while CFA has potential in many other contexts related to predation conflict where no other non-lethal method has proven to be effective (Tobajas et al., 2020c; Snijders et al., 2021). In any case, in our study system, the CC appears a promising approach for protecting waterfowl nests from predation. Whether or not the effect size of CC was meaningful for the waterfowl conservation remains, however, to be studied. The decline in nest predation by red foxes was quite strong in CC sites (over tenfold decrease compared to control sites), but it has to be remembered that predation level of artificial nests likely differs from that of natural nests (Pärt and Wretenberg, 2002). Norbury et al. (2021) however showed that CC increased reproductive success in natural nests of waterfowl.

4.1. Management implications

Our study provides evidence that non-lethal methods offer an alternative approach to the removal of predators to reduce predator impacts on their prey (e.g. Gustavson et al., 1974; Tobajas et al., 2020a; Norbury et al., 2021). This improves the possibilities of predator management. In our case, the chemical camouflage approach show particular promise to protect declining waterfowl species from nest predation, although the response of mesopredators was species-specific. Managers planning the use of non-lethal methods should thus carefully consider the

effectiveness and response of their focus predator on different methods. We, nevertheless, encourage for a wider use of non-lethal methods in reducing predator impact on their prey, especially in systems where red foxes are important nest predators. Other potential applications of these techniques include protecting pulses of prey (e.g. synchronously nesting birds or reptiles, such as turtles), reducing predation soon after translocation of endangered species, reducing the consumption of anthropogenic food (e.g. waste) or even reducing the impact of herbivores and granivores raiding seed species (Snijders et al., 2021; Price et al., 2022). Importantly, these methods offer an ethical and potentially effective approach to maintain native predator fauna, but still protect vulnerable prey at risk from scent hunting predators.

CRediT authorship contribution statement

V. Selonen: Conceptualization, Data curation, Formal analysis, Writing – original draft. **P.B. Banks:** Conceptualization, Writing – review & editing. **J. Tobajas:** Conceptualization, Writing – review & editing. **T. Laaksonen:** Conceptualization, Funding acquisition, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability statement

The datasets generated during and/or analysed during the current study are available from the first author.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2022.109749>.

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