Alien Predation in Wetlands – the Raccoon Dog and Waterbird Breeding Success

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Abstract

Alien predators are known to potentially strongly affect their prey populations. We studied the impact of raccoon dogs (*Nyctereutes procyonoides*) on waterbird breeding success in eight semi-urban wetlands in Finland. We manipulated raccoon dog density in two wetlands by removing individuals (2002 protection year, 2003 and 2004 removal years). We additionally performed nest predation experiments. We monitored raccoon dog density, estimated hunting bag size and observed waterbird breeding success. Our hypothesis predicts that the omnivorous raccoon dog plays a role in waterbird breeding success by depredating nests. Our experiments shown that the raccoon dog hunting bag in eutrophic wetlands may be large, as we removed 8.6–20.0 animals per km^2. Both our nest predation experiment and field data indicated that raccoon dogs affect the breeding success of waterbirds. We found a significant relationship between raccoon dog density index and predation rate of the artificial nests, but not between red fox (*Vulpes vulpes*) density and predation on artificial nests. We did not find an association between raccoon dog abundance and the breeding success of mallards (*Anas platyrhynchos*) and great crested grebes (*Podiceps cristatus*). However, our study shows that birds species with different breeding strategies – e.g. great crested grebe, mute swan (*Cygnus olor*), mallard, Eurasian wigeon (*Mareca penelope*), coot (*Fulica atra*), lapwing (*Vanellus vanellus*) and marsh harrier (*Circus aeruginosus*) – when considered together showed higher breeding success both in 2003 and 2004 when compared to breeding success before removal. There was, however, variation in how strongly the species responded to raccoon dog removal. Our results indicate that the removal of alien raccoon dogs can be an important tool in wetland management.

Keywords: ducks, invasive species, lapwing, nest predation experiment, *Nyctereutes procyonoides*, predator removal

Introduction

Predators are known to often limit their prey populations, and alien predators in particular do so (Salo et al. 2007, 2010). Among invasive alien species, mammalian predators are a group that strongly affect their novel environments and have even caused the extinctions of many prey species (Blackburn et al. 2004, Bodey et al. 2011, but see Smith et al. 2010). Worldwide, the feral cat (*Felis silvestris catus*) is the most harmful alien predator (Medina et al. 2011). Other notorious species include the feral dog (*Canis lupus familiaris*), red fox (*Vulpes vulpes*), stoat (*Mustela erminea*) and American mink (*Neovison vison*) along with rats (*Rattus* spp.) (Courchamp et al. 2003, Towns et al. 2006, Doherty et al. 2015).

In general, control and eradication programmes have been most successful on islands, whether involving native red foxes (Marcström et al. 1988) or alien cats or rats (Nogales et al. 2004, Russell and Holmes 2015). For example, the mortality of black-vented shearwaters (*Puffinus opisthomelas*) on Natividad Island was lower and the breeding success of small petrels higher on Marion Island after cat eradication (Cooper et al. 1995, Keitt and Tershy 2003). Likewise, local American mink eradication in Northern Europe has also been successful; many waterbird populations, e.g. tufted duck (*Aythya fuligula*), ringed plover (*Charadrius hiaticula*) and black guillemot (*Cepphus grylle*) clearly increased when minks were removed from the islands of an archipelago national park in Finland (Nordström et al. 2002, 2003). Predator control has faced problems in many cases (Smith et al. 2010, Bodey et al. 2011), although short-term predator removal has sometimes been successful even in continental areas, especially in agricultural habitats (Norrdahl and Korpimäki 1995, Bolton et al. 2007).

The raccoon dog (*Nyctereutes procyonoides*) is an invasive alien predator spreading relatively rapidly to new areas in Europe (Helle and Kauhala 1991, Kauhala and Winter 2006). In Finland, the yearly hunting bag of raccoon dogs increased over a period of 20 years from 60 000 (in 1996) to over 200 000 (in 2016); the latter is over four times the number of bagged red foxes and twice the number of mountain hares (*Lepus timidus*) (Luke 2017). This has raised concerns of the effects this predator is having on native fauna (e.g. Viksne et al. 2005, Fox et al. 2016, Pöysä et al. 2019) and, further, the need to control its numbers in Europe (Bern Convention 2009). In 2017, the European Commission placed the raccoon dog on the list of invasive alien species of Union concern (Europen Union 2017). However, the role of raccoon dog on the breeding success of ground-nesting birds is still poorly understood (but see Krüger et al. 2018).

The effects of raccoon dog predation on grouse and ducks has been studied using a removal experiment in oligotrophic areas in southern Finland (Kauhala et al. 2000, Kauhala 2004). However, the hunting bag and its effect on raccoon dog population density remained low in this experiment, conducted in a large removal area in a boreal forest, possibly partly because of continuous immigration of animals from nearby areas. As the earlier attempt to lower raccoon dog density has been unsuccessful, in this study we aim to design and carry out a successful raccoon dog removal in eutrophic wetlands, and to study its effects on the breeding success of waterbirds by monitoring predation rates of artificial nests along with examining in bird nesting success.

The diet of the raccoon dog in eutrophic or other bird-rich wetlands, such as our study area, has not been well studied. However, some results indicate a diverse diet, including eggs of ground-nesting birds (Kauhala and Auniola 2001, Eronen 2007). Therefore, although the raccoon dog is often considered an inefficient predator, it may impact the nesting success of waterbirds if its population size increases to high levels. Eutrophic wetlands close to rural areas, where natural and anthropogenic food resources are abundant, are an example of areas where raccoon dog densities may be very high.

Here we experimentally study, for the first time, the impact of the invasive raccoon dog on bird nesting success in eutrophic wetlands. The wetland area inhabited by many rare bird species (Leivo et al. 2002) has strongly decreased in Europe during the last 100 years (Čížková et al. 2013). In Finland, waterfowl populations have especially decreased in eutrophic wetlands (Lehikoinen et al. 2016), and many species living in these habitats have become threatened (Lehikoinen et al. 2019). We hypothesize that the raccoon dog affects waterbird breeding success mainly by predating their nests, and that reducing raccoon dog density with removal will enhance the breeding success of waterbirds. We first examined the effects of raccoon dog and red fox density on the nest predation rate of artificial nests. We then separately investigated the relation between raccoon dog density and mallard and great crested grebe breeding success in the study area. Finally, we analysed the impact of raccoon dog removal on bird nesting success (all study species together).

Material and Methods

Removal wetlands

Our removal sites in wetlands were located around the Helsinki metropolitan area. We used two wetlands in the predator removal experiments (name and number of wetland are presented in Table 1, Figure 1). These were eutrophic sea bays with dense vegetation, which are also internationally important bird areas. Common reed (*Phragmites australis*) was the main plant species in these areas. Both removal areas are 4.5 km apart from the nearest control wetlands in our study. In eutrophic areas, raccoon dog home ranges average approximately 1 km^2 in size (Choi and Park 2006, Kauhala et al. 2010), and thus, predator removal had hardly any effect on raccoon dog abundance in our control wetlands.

In removal wetland 1 (Laajalahti), the size of the predator removal area was 2.0 km^2 (Table 3). This area consisted of dense reed beds, forest, open meadows and shore meadows pastured by cows. The size of predator removal wetland 2 (Vanhankaupunginlahti) was 3.5 km^2. This area consisted of a mosaic of cultivated fields, dense reed beds, shore meadows and forest patches. Most of the wetlands in both of these predator removal areas are protected.

We also had the possibility of using two other wetlands as removal areas. However, deviating from the original plan in Östersundom (area 7 in Table 1), hunters carried out intensive raccoon dog removal already during the first study year when racoon dog hunting was not allowed in our experiment. Raccoon dog density index was 0 at this site after the hunting season, and, thus, we could no longer use the wetland as a removal area. We used this wetland only in the nest predation experiment (Table 1). Suomenoja (area number 8 in Table 1) was not suitable as a removal wetland because the potential removal area was too small (only 30 ha) for effective raccoon dog removal. This wetland is also used only in the nest predation experiment (Table 1).

Control wetlands

We used two control wetlands, both of which consisted of two areas (Table 1, Figure 1). In these cases, the two areas had to be combined to acquire enough data on bird breeding success. Control wetlands 1 and 2 were situated in the eastern and western edges of the Helsinki metropolitan area, respectively. The control wetlands contained habitats similar to those of the predator removal wetlands; both were eutrophic and in their vegetation the common reed predominated. However, their bird communities had fewer species and the numbers of breeding birds were lower than in our predator removal wetlands. Both control wetlands are surrounded by urban settlement, as are our predator removal wetlands.

Bird surveys

We used brood per pair indices because they provide a good estimate of the females in precocial birds that had avoided nest predation (Nummi and Pöysä 1995). Annual variation in nest predation rates could be followed with these indices. We could compile three years of nesting success data from five precocial bird species in both removal wetlands: the mallard (*Anas platyrhynchos*), great crested grebe (*Podiceps cristatus*), Eurasian wigeon (*Mareca penelope*), mute swan (*Cygnus olor*) and coot (*Fulica atra*). We also gathered data on the lapwing (*Vanellus vanellus*) and the altricial marsh harrier (*Circus aeruginosus*) from one of the removal wetlands. In the control areas, we collected data for mute swan, mallard and great crested grebe. Waterfowl counts were performed as a combination of point and round counts. The methods allowed us to properly count the entire study areas (see Koskimies and Väisänen 1998). The timing of spring was taken into account in both the pair and brood counts (Koskimies and Väisänen 1998). Pair counts were performed three times during the period April 25–June 6. In waterfowl brood counts, the size and age of each brood was determined using the classification of Pirkola and Högmander (1974). This makes it possible to differentiate among broods. We performed brood counts three times during early July. In the control areas, we only have data for mute swan, mallard and great crested grebe.

Table 1. Wetlands and their use in our study. Data of control areas 3 and 4 are pooled as control wetland 1, and that of control area 5 and 6 are pooled as control wetland 2

Wetland	Raccoon dog removal wetlands	Control wetlands	Nest predation experiment wetlands	Predator density
1 Laajalahti	x		x	x
2 Vanhankaupunginlahti	x		x	x
3 Pitkäjärvi		x	x	x
4 Vartiokylänlahti		x	x	x
5 Kaitalahti		x	x	x
6 Espoonlahti		x	x	x
7 Östersundom			x	x
8 Suomenoja			x	x

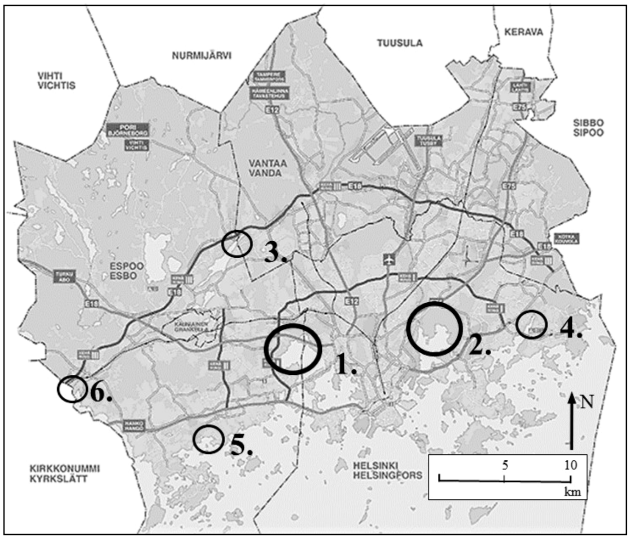

Figure 1. Distribution of predator removal wetlands (large circles 1 and 2 on the map), control wetland 1 (small circles 3 and 4 on the map) and control wetland 2 (small circles 5 and 6 on the map); see also Table 1

Predator density index

Signposts (similar to track plates) were used to follow the relative abundance of predator populations in the study areas (Lindhart and Knowlton 1975, Kauhala 1994, Meckstroth and Miles 2005). The signposts were made of sand that was loosened and raked. The signpost area was ca. 1 m^2 and circular in shape. A chemical lure that attracts predators was placed in the middle of the post. We used the commercial lure Grey Ambush (J.R. and Sons, Monroeville, OH, USA), made of grey fox (*Urocyon cinereoargenteus*) scent glands. We dipped a 25-cm-long wooden stick in the lure and placed it in the middle of the signpost. The attractant has effectively lured raccoon dogs in earlier methodological studies (Kauhala 1994). The signposts were prepared during the day; nocturnal animals visited the posts during the night and left their tracks in the sand bed.

We placed 10 signposts in each of the predator removal (n=2), control (n=4) and two other eutrophic wetlands in the Helsinki area (Table 1). The posts were placed at a distance of at least 500 m between each other (see Meckstroth and Miles 2005) and were checked daily for five days from late May to early June. Animal tracks left in the sand were identified and counted. The timing of the experiment was chosen so that the raccoon dog and fox litters had not yet left their dens. The same signpost areas were used in each study wetland during 2002–2004; thus, the density indices of the predators were comparable between years and indicated the change in predator abundance.

Nest predation experiment

To test the hypothesis that nest predation rate increases when raccoon dog densities increase, we conducted an experiment with 10 artificial nests and repeated it in each study area during the period of 2002–2004 (Table 1). We acknowledge that the nest predation rate of artificial nests is not equal with natural nests (see Krüger et al. 2018). The nest predation experiments give rough estimates of nest predation rate, which are generally higher than those of natural nests (Valkama et al. 1999, Väänänen 2000). However, artificial nests give an index of the nest predation rate, and this has recently been used to compare nest predation in a number of experimental designs (e.g. Carpio et al. 2016). Artificial nest experiments are also useful for formulating hypotheses. We performed the nest predation experiment in the same eight wetlands used to collect data for raccoon dog and red fox densities (signposts, Table 1). The experiments were performed after mid-May during the natural incubation time of ducks. The nests were checked 2, 8 and 16 days after the beginning of the experiment.

Maps of the study areas were used to sketch the placement of artificial nests. The actual locations of the nests were chosen in the field, as we wanted to place each nest in a site typically used by mallards. Detritus, dry hay and several down feathers of ranched mallards were mixed and placed to cover each artificial nest. Rubber gloves were used in all handling and finishing of the nests to minimize the human scent. During the next day, two hen (*Gallus domesticus*) eggs were placed in the nest and the eggs were covered with nest material, as female ducks do when they leave their nests. The nest was counted as plundered if the eggs were missing or the eggshells broken. Because our experiment imitated the nests of mallards and other dabbling ducks (e.g. cover of grass or small bushes), it was impossible to find any paw prints that would have revealed the nest predator. However, if eggs were not missing, in certain cases it was possible to distinguish the tooth size of the predator from the eggshells. Mammalian predators (raccoon dog sized) were in certain cases identified as the predator.

Our goal was to determine the average nest predation rate in each study wetland. The nests were placed app. 10 m from the shore zone and at least 100 m from the nearest artificial nest. We assumed that the distance of 100 m was sufficient to enable us to consider the predation risk of each nest independently of the other nests (see Valkama et al. 1999). We found no sign of predators or major predation during the nesting trials. This was expected, because there was much human activity in the wetlands. Thus, mammalian predators were unlikely to associate the artificial nests with signs of unusual activity. Our nest predation experiment shows the potential nest predation risk especially for species nesting within the shore area (e.g. lapwing, teal, wigeon and partly mallard). It also only gives a general insight into nest predation at our study wetlands.

Predator removal

All of our study wetlands have annually breeding populations of raccoon dog, red fox, hooded crow (*Corvus corone cornix*) and magpie (*Pica pica*). A few other uncommon or rare predators additionally inhabit the areas (see Table 2). In our removal wetlands, predators were first protected during the hunting season in 2001/2002. During the next two hunting seasons, the predators were hunted as effectively as possible with legal hunting methods. The raccoon dog was our main target for predator removal, but low numbers of American mink and red fox were also removed. Hooded crows were not hunted, and we assume that crow populations were stable during the whole study period.

Table 2. Rough abundance of most common mammalian and avian predators in the study wetlands. Based on Lindén et al. 1996, Valkama et al. 2011, pers. obs.). Explanations of the numbers: 1 = Laajalahti, 2 = Vanhankaupunginlahti, 3 = Pitkäjärvi, 4 = Vartiokylänlahti, 5 = Kaitalahti, 6 = Espoonlahti, 7 = Östersundominlahti, 8 = Suomenoja

Raccoon dog *Nyctereutes procyonoides*	Red fox *Vulpes vulpes*	Badger *Meles meles*	American mink *Neovison vison*	Pine marten *Martes martes*	Hooded crow *Corvus corone cornix*, Magpie *Pica pica*
1.very common	common	few	few	-	very common
2. very common	common	few	few	rare	very common
3. very common	common	few	few	-	very common
4. very common	common	few	few	rare	very common
5. very common	common	few	few	-	very common
6. very common	common	few	few	-	very common
7. common	common	few	few	rare	very common
8. very common	common	few	few	-	very common

Predator removal was performed as voluntary work by local hunters. Hunting was in operation between August 1 and April 20 (during the legal hunting season of raccoon dogs). Raccoon dogs were mostly hunted using live traps, although shooting using fish carrion as bait was also quite common. Earth dogs and other types of hunting dogs were also used. All these hunting methods are legal in Finland. Captured badgers (*Meles meles*) were set free from traps.

Statistical methods

The daily predation rates of the artificial nests were calculated using the Mayfield method (Mayfield 1961), and daily visitation rates were used for calculating raccoon dog density indices. We then used linear regression to study the association between raccoon dog density (signpost indices) and the predation rate of artificial nests. The same analysis was also conducted to study the association between red fox density and nest predation rate. Data for raccoon dog density, red fox density and nest mortality rate were collected from all eight wetlands for years 2002–2004 (Table 1). Thus, the total number of data points in the linear regression is 24 (eight wetlands times three years). Linear regression was also used to study the effect of raccoon dog density on the nesting success of mallards and great crested grebes (separately). The number of broods per pair was used as an index for nesting success. Sufficient data for nesting success were acquired from six areas for years 2002–2004 (Suomenoja and Östersundom had insufficient data for nesting success). Thus, the number of data points for the linear regression was 18. For both tests, the results were considered significant at $P < 0.05$, and the Shapiro-Wilk test was used to test the normality of the residuals. Statistical analysis was performed using SigmaPlot software version 11.0 (SyStat 2008).

The effect of raccoon dog control on the overall breeding success of waterbirds with different breeding strategies was tested using the non-parametric Wilcoxon signed-rank test. Changes in the brood/pair index from the protection year (2002) to predator removal years 2003 and 2004 was tested separately. All observations (broods/breeding pair in each species) were considered asone observation. Thus, as data for the change in lapwing and marsh harrier breeding success were acquired only from removal area II, the number of observations was 12 (N = 12 in all Wilcoxon signed-rank tests). The test was not performed for control areas due to the very low number of observations acquired from those areas (N=6).

Results

Raccoon dog hunting bag and density index

The raccoon dog hunting bag was large; we harvested 8.6–20.0 raccoon dogs per km^2 per year during the hunting seasons (altogether 158 raccoon dogs, Table 3). In addition, five American minks and nine red foxes were captured.

Table 3. Number of bagged raccoon dogs and bag per km^2 divided for the three hunting periods: 2002 (no hunting); I = Aug 1, 2002–Apr 30, 2003; III = Aug 1, 2003–Apr 30, 2004.

Removal wetland	Area, km^2	Raccoon dog bag			Bag per km^2		
		I	II	III	I	II	III
1 Laajalahti	2.0	-	21	37	-	10.5	18.5
2 Vanhankaupunginl.	3.5	-	30	70	-	8.6	20.0
Total	5.5	-	51	107	-	9.3	19.5

Our signpost monitoring indicates that we succeeded in manipulating raccoon dog densities (Table 4). In the control wetlands (no hunting), the values of the signpost indices decreased slightly, while density indices in the raccoon dog removal areas collapsed (Table 4). This decrease was not very clear after the first hunting season, even though we succeeded in capturing approximately 10 raccoon dogs per km^2 (Table 3). However, after the second removal season, the raccoon dog density index was only 12% of the year 2002 value preceding the removal. Compared to control areas, raccoon dog densities were higher in the removal areas prior to removal but lower after it.

Table 4. Density index of raccoon dog's and red foxes (observations per 10 signpost days) in removal wetlands and control areas. Predator protection year was 2002 (bold) and removal years 2003 and 2004. Predator hunting was not carried out in the control areas. Names of removal and control areas are shown in Table 1.

	Raccoon dog, *Nyctereutes procyonoides*			Red fox, *Vulpes vulpes*		
Area	**2002**	2003	2004	**2002**	2003	2004
Removal wetlands						
1	**4.60**	2.60	0.20	**0.00**	0.40	0.00
2	**2.20**	2.20	0.60	**1.40**	0.20	0.40
Mean	**3.40**	2.40	0.40	**0.70**	0.30	0.20
Control wetlands						
1	1.30	0.80	1.00	0.40	0.20	0.20
2	1.20	1.60	1.10	0.50	0.10	0.40
Mean	1.25	1.20	1.05	0.45	0.15	0.30

Nest predation experiment

Our nest predation experiment showed strong association between raccoon dog density (signpost index) and the proportion of nests preyed upon (Figure 2). The linear regression of raccoon dog density on nest predation rate was significant ($R^2 = 0.301$, $P = 0.006$, Figure 2) and the residuals did not differ from the normal distribution (Shapiro-Wilk test, $P = 0.604$). In contrast to raccoon dog, the linear regression between red fox density and nest predation rate was not significant ($R^2 = 0.022$, $P = 0.489$).

Effect of raccoon dog removal on bird nesting success

The linear regression of raccoon dog density on the nesting success of mallard ($R^2 = 0.6 \times 10$^-6, $P = 0.992$) or great crested grebe ($R^2 = 0.0488$, $P = 0.378$) were not significant. As a whole, however, our study birds with different breeding strategies (precocial and altricial ones) showed improved breeding success both in 2003 (Wilcoxon signed-rank test, $P = 0.028$) and 2004 ($P = 0.023$) compared to their success before removal (Table 5). In the control area, the breeding successes of the three study species were nonuniform: it increased in one species, was stable in the second and slightly decreased in the third one (Table 5).

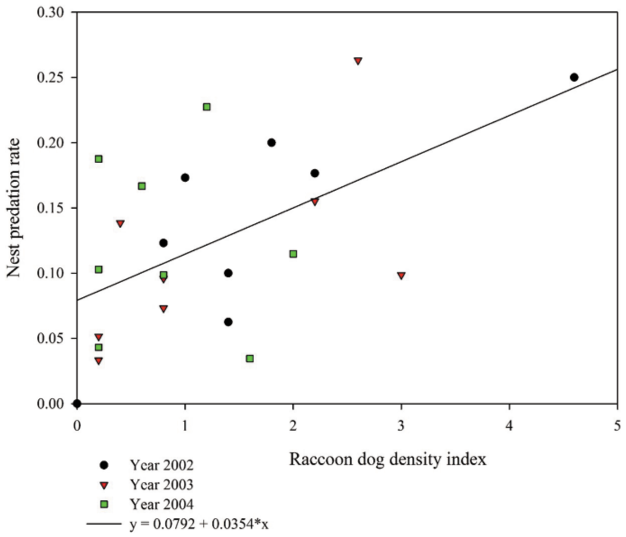

Figure 2. Results of the association between the raccoon dog density index and the nest predation experiment after 16 days from the start of the experiment in years 2002–2004. The figure shows the relation between the raccoon dog density index and the daily mortality rate of the artificial nests in eight wetlands (linear regression, $R^2 = 0.301$, $P = 0.006$)

Table 5. Brood/pair index of birds in raccoon dog removal wetlands I and II as well as in control wetlands 1 and 2 in 2002-2004. The breeding numbers of birds are shown in parentheses. Names of the removal and control areas are shown in Table 1

Species	Removal wetland I			Removal wetland II		
	2002	2003	2004	2002	2003	2004
Great crested grebe	0.365	0.317	0.397	0.169	0.651	0.238
Podiceps cristatus	(63)	(62)	(63)	(71)	(43)	(63)
Mute swan	0.143	0.667	0.200	0.500	1.000	1.000
Cygnus olor	(7)	(3)	(5)	(4)	(2)	(4)
Mallard	0.135	0.325	0.139	0.176	0.269	0.130
Anas platyrhynchos	(74)	(40)	(72)	(136)	(78)	(123)
Wigeon	0.150	0.400	0.300	0.308	0.071	0.286
Mareca penelope	(20)	(10)	(10)	(13)	(14)	(14)
Coot	0.077	0.389	0.263	0.583	0.737	0.556
Fulica atra	(13)	(18)	19)	(12)	(19)	(18)
Lapwing	-	-	-	0.000	0.000	1.000
Vanellus vanellus	-	-	-	(3)	(3)	(6)
Marsh harrier	-	-	-	0.000	0.000	1.000
Circus aeruginosus	-	-	-	(1)	(1)	(1)

Species	Control wetland I			Control wetland II		
Great crested grebe	0.182	0.364	0.667	0.154	0.400	0.538
Podiceps cristatus	(11)	(11)	(22)	(18)	(10)	(10)
Mute swan	1.000	1.000	-	1.000	1.000	1.000
Cygnus olor	(1)	(1)	-	(1)	(1)	(2)
Mallard	0.269	0.208	0.434	0.263	0.071	0.167
Anas platyrhynchos	(26)	(24)	(23)	(19)	(11)	(12)

Discussion

Raccoon dog removal

To our knowledge, the present study of alien mammalian predator removal is the first experimental one to be conducted in inland eutrophic wetlands, the habitat type, in which the most pronounced effects of raccoon dog predation on waterbirds have so far been found (Naaber 1974, Mikkola-Roos and Yrjölä 2000, Viksne et al. 2005). Despite the limited size of our predator removal areas, we succeeded in decreasing the density of local raccoon dog populations. With dense predator populations or small removal areas which are free to be recolonized, this is not easily achieved, and, indeed, has not been achieved earlier with raccoon dogs (e.g. Kauhala et al. 2000, Kauhala 2004, Meckstroth and Miles 2005, Bodey et al. 2011). Alien predators have sometimes been especially problematic when provided with alternative food sources along with the native species that they affect (Courchamp et al. 1999, Doherty et al. 2015). Alternative food in the form of anthropogenic refuse very likely helps predators, e.g. raccoon dogs, to build up high population densities in bird-rich wetlands surrounded by urban settlement and enable them to survive during seasons when most birds are absent (see Newsome et al. 2015). In our case, the relatively small removal wetland areas may have been one reason behind the success of removal. In smaller wetlands, the hunting pressure and hunting bag relative to the size of the removal area may be very great. In our study, the hunting bag was 8.6–20.0 animals per km^2, whereas in a previous Raccoon Dog removal experiment it ranged from 0.7 to 1.4 animals per km^2 (Kauhala 2004).

The abundance index of raccoon dog clearly declined in 2004 compared to pre-removal and even to the first removal period of 2003, and has since remained low (Väänänen and Nummi, unpubl.). This apparently was a result of large bag numbers in 2003/2004. Thus, we achieved the first goal of our experiment, i.e. a reduction in the local raccoon dog population. The raccoon dog removal wetlands receive a continuous inflow of individuals from outside the removal area, although the urban areas around the wetlands may somewhat slow down these movements.

In a previous archipelago experiment on American mink removal, the catch was over 60 individuals during the first control year and only around 10% of that during the following seven years (Nordström et al. 2002). In our study, the raccoon dog density index collapsed after the second hunting season and was only approximately 12% of the value preceding the removal. In a predator removal area in the boreal forests of southern Finland, hunting of small and medium-sized predators had no consistent impact on predator populations or prey (Kauhala 2004).

As our predator removal experiment shows, effective predator control is very laborious, e.g. hunting a single raccoon dog in our study wetlands took 11.1 h with a dachshund (Nurmi 2004). If the goal is to reduce predator densities, a considerable amount of time, various hunting methods and skilful hunters are needed. Raccoon dog density may be very high in eutrophic wetlands, and raccoon dogs readily recolonize the removal area if hunting is discontinued.

Bird breeding success

As predicted, artificial nest survival was lower in areas of high raccoon dog density indices, whereas nest survival did not respond to fox density indices. We have similar results from a recent experimental study on nest predation in agricultural landscapes in southern Finland: we did not have any observation of red fox predation in an artificial nest survey by cameras, whereas the raccoon dog was the most common medium-size predator of artificial study nests (Krüger et al. 2018). However, both mesopredators commonly visited signposts (revealed with trap camera) in the same study areas. In the archipelago of northern Sweden, results of a nest predation experiment indicate the important role of raccoon dogs in nest survival. When raccoon dogs were present, nearly every artificial and natural nest was predated on the islands, whereas nest survival was high when raccoon dogs were absent (Dahl and Åhlén 2018). Dahl and Åhlén (2018) concluded that nest predation by the raccoon dog was additive in the outer archipelago. Data by Ruuska (2018) (wildlife camera survey in an agricultural landscape in southern Finland) indicated the same phenomenon. His results showed that nest predation caused by the raccoon dog correlated positively with raccoon dog visits at signposts.

The effect of raccoon dogs was also visible in some of the bird data: nesting success tended to increase in certain bird species studied after successful raccoon dog removal, although there was much inconsistency in the results. In some cases, as with the lapwing and coot, breeding success clearly improved, while in others, as with the mallard and European wigeon, it increased only marginally or not at all. It is worth noting that the nest site requirements of the species studied here vary considerably. Especially mallards are very flexible in their nest site requirements and may build their nests far from water even in urban settings (Väänänen et al. 2016); this may dilute the nest predation risk and the effect of the removal of a single predator. The experimental nests, again, were near the shore, which is very likely why predation rates there were more closely associated with raccoon dog density. Lapwings, on the other hand, can only nest in open land adjacent to wetlands in our study areas. During the removal period, no consistent increase in the breeding success of different species was found in the control areas. Data covering more years would probably have given clearer results in our study because year-to-year variation often occurs in the breeding success of waterfowl (Pöysä et al. 2006).

Of individual species, lapwings are known to be very vulnerable to predation, as their nests are placed in sparse vegetation. The nests of lapwings breeding at low densities, as was the case in our study area, are more likely to suffer predation than those breeding at high densities (Elliot 1985, Berg et al. 1992, Seymour et al. 2003). We also have direct evidence of raccoon dog predation. Adjacent to our control wetland (1 km apart), two raccoon dogs predated a lapwing nest in an agricultural field (Anna-Maija Myllynen, in litt.). In an intensive study in England, the predator control was more likely to result in increased nest survival at sites where predator densities (foxes, crows) were high (Bolton et al. 2007). It is noteworthy that raccoon dogs attain higher densities than foxes. In southern Finland, raccoon dog densities have been found to be 2.2 times higher than those of red foxes (Kauhala et al. 2006).

We should note that our urban wetlands are a system of relatively complicated predator-prey interactions that we could only partly manipulate (Ellis-Felege et al. 2012, Doherty et al. 2015). These include corvids, numerous in wetlands and urban areas and well known for their nest-robbing activities of ground-nesting birds (Väänänen 2000, Jokimäki and Huhta 2000, Sorace and Gustin 2009, Krüger et al. 2018). Predatory birds often cannot be manipulated, and therefore the breeding success response of birds have been meagre (Meckstroth and Miles 2005, Lloyd 2007) or variable (Bolton et al. 2007, Bodey et al. 2011) in many predator removal studies in complex ecosystems. In our study, we assume that the observed increase in the nesting success of waterbirds is mostly a result of the raccoon dog removal. The nesting success of waterbirds increased after large raccoon dog bag numbers (and a drop in the raccoon dog density index). During the same period, the density index of red fox was more or less stable. Moreover, the numbers of removed foxes and minks were very low compared to the raccoon dog (nine and five, respectively, compared to 158), and, finally, the success of experimental nests appeared not to respond to fox density although it did respond to that of raccoon dogs. Unlike red foxes, raccoon dogs use wet reed beds for both hunting and resting (Väänänen et al., unpubl. radio telemetry data). So, waterbirds nesting in reed beds are vulnerable to raccoon dog predation especially when the water levels are low. Corvids were not hunted in our study wetlands and the breeding numbers of hooded crows appeared stable. Predation by corvids may have been one reason why certain waterbird species did not respond very clearly to the raccoon dog removal.

The effect of our raccoon dog removal was not as strong as that found in the mink control programme in the Finnish archipelago (Nordström et al. 2002). This may partly be because archipelago birds have shown higher levels of naiveté to alien predation (Banks and Dickman 2007). The American mink in the archipelago seems to represent a case of level-1 naiveté (*sensu* Banks and Dickman 2007) of prey, in which it adopts no proper antipredator behaviour. This was shown especially for the black guillemot (Hario 2002), apparently because previously mammalian predators have not occupied the outer Baltic archipelago. On the other hand, probably only level-3 naiveté in mainland birds occurs with the raccoon dog, where prey recognize the predator as dangerous – the raccoon dog is outwardly not very different from the red fox or badger. However, the raccoon dog population is denser than that of these native mesopredators, especially in southern and central Finland (Kauhala et al. 2006). Therefore, raccoon dogs may affect nesting birds simply because of their large numbers.

We recognize that most bird species in our study do not show a very strong response to raccoon dog removal. We still think that it is worth considering, and, we encourage wildlife managers to consider the need of alien predator removals in important bird areas so as not to waste the effect of other conservation measures, e.g. habitat restoration (see Bolton et al. 2007). Without effective alien predator control, habitat restoration may often not be very beneficial for many waterbirds, such as lapwing (Bolton et al. 2007), dunlin (*Calidris alpina schinzii*) (Osara 2002), bittern (*Botaurus stellaris*) (White et al. 2006), common pochard (Fox et al. 2016), or black-headed gulls and waterfowl (Pöysä et al. 2019).

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