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# Removal of medium-sized predators and the breeding success of ducks in Finland

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A b s t r a c t . A predator removal study was done in Finland to reveal the possible effects of mammalian predators on the breeding success of ducks. Predator removal/protection from hunting was most effective in northern Finland. Also in eastern Finland predator removal had some influence on predator numbers, whereas its impact on predator numbers was not so evident in southern Finland. In southern Finland, no increase in the breeding success of ducks was observed in the predator removal area, whereas in northern Finland the relative reproduction rate of diving ducks increased in the removal area and that of dabbling ducks declined in the control area. In eastern Finland, the breeding success of ducks declined in both areas. There was a positive relationship between the raccoon dog index and the relative reproduction rate of dabbling ducks in southern Finland, indicating that raccoon dog numbers probably are of minor importance for the breeding success of ducks. On the contrary, there was a negative relationship between the fox and marten indices and the breeding success of ducks in some areas. Marten and fox removal may thus have a positive effect on the breeding success of ducks in Finland. The effect of the American mink could not be verified in this study.

**Key words:** American mink, pine marten, raccoon dog, red fox, duck breeding success, predator removal

## Introduction

Predation is often considered a major factor affecting the breeding success of water birds (C o w a r d i n et al. 1985, K l e t t et al. 1988, B a l l et al. 1995, G r e e n w o o d et al. 1995, M a x s o n & R i g g s 1996, F e r r e r a s & M a c d o n a l d 1999, O p e r m a n i s et al. 2001, N o r d s t r ö m et al. 2002, 2003). Both mammalian and avian predators may be involved (J o h n s o n et al. 1989, P a i n e et al. 1990, O p e r m a n i s et al. 2001), although mammals are often considered to be more important (reviewed in B e l l e b a u m 2002). To test the effect of predators on duck productivity, several predator removal experiments have been done with variable success (e.g. L o k e m o e n & W o o d w a r d 1993, C l a r k et al. 1995, S a r g e a n t et al. 1995, G a r r e t t s o n et al. 1996, G a r r e t t s o n & R o h w e r 2001). Most of these studies have been conducted in the Prairie Pothole Region of North America. C ô t é & S u t h e r l a n d (1997) analysed the results of 20 predator removal studies and found that predator removal increased the autumn densities of bird species, *i.e.* affected the breeding success of birds, but the effect of predator removal on breeding population sizes was not significant. Also B a r t o s z e w i c z & Z a l e w s k i (2003) found that although American minks *Mustela vison* destroyed many waterfowl nests, the arrival of mink has not resulted in a decrease in waterfowl populations.

These kinds of studies are almost absent from Europe. In spite of a lack of knowledge, hunting of small and medium-sized carnivores is considered good game management and is widely recommended by hunting organisations in Finland and other countries. Knowledge

of the true impact of predators on native fauna, like waterfowl, is thus needed. The roles of the raccoon dog *Nyctereutes procyonoides* and the American mink – introduced carnivores in Europe – are especially interesting, because alien predators are known to have caused much damage on native fauna (e.g. E b e n h a r d 1988). The raccoon dog is among the most common carnivores in southern Finland, and the mink is common all over the country.

The aim of the present experimental study was to examine the impact of predator removal on the breeding success of ducks in the inland waters of southern, eastern and northern Finland. We removed/protected from hunting medium-sized mammalian predators in three areas with partly different carnivore communities and monitored the breeding success of ducks for 4–5 years after the initiation of the experiment. The predictions, mainly based on the above mentioned studies, were: 1) the breeding success of ducks will increase in removal areas and decrease in control areas, 2) the effect of predator removal on duck breeding success will be greatest in southern Finland where both introduced predators (raccoon dogs and minks) are common and 3) the impact of raccoon dog removal will be seen especially in the breeding success of ground-nesting dabbling ducks.

This study is a part of a larger experimental work designed to evaluate the impact of predator removal on game animals. The results of the effect of predator removal on hares and grouse have been published earlier (K a u h a l a et al. 1999, 2000).

## Methods

### S t u d y a r e a s a n d e x p e r i m e n t a l d e s i g n

The study was performed between 1993 and 1998 in southern Finland and between 1993 and 1997 in eastern and northern Finland (K a u h a l a et al. 1999: Fig. 1). In each region there was a predator removal area where predator hunting was intensive, and a control area where medium-sized carnivores were not hunted. The sizes of predator removal and control areas were 55 km$^2$ and 48 km$^2$, 72 km$^2$ and 106 km$^2$ and 100 km$^2$ and 116 km$^2$ in southern, eastern and northern Finland, respectively. The distance between the removal and control areas was at least 5 km. All areas were within the boreal forest zone and included many lakes, ponds and some small rivers. In northern Finland most lakes were shallow and eutrophic, while in the other areas most lakes were oligotrophic.

The predators included in the experiment were the raccoon dog *Nyctereutes procyonoides*, red fox *Vulpes vulpes*, pine marten *Martes martes* and the American mink *Mustela vison*. Raccoon dogs were rare in eastern Finland and absent in northern Finland. Other predators occurred in all areas. Voluntary hunters were responsible for predator removal. Common methods (traps, foot snares, shooting from a bait) were used during the normal hunting season (for raccoon dogs, red foxes and minks from 1 August to 30 April, for pine martens from 1 November to 31 March). Predator removal was initiated in the autumn of 1993.

### M o n i t o r i n g p o p u l a t i o n s

Fox and marten populations were monitored each winter by using snow track counts. Experienced field assistants together with the local hunters counted the snow tracks once each winter (between 15 January and 15 March) from transect lines, oriented from south to north, using the wildlife triangle method (L i n d é n et al. 1996). The transect lines covered the whole study areas, the distance between them being 500 m in southern Finland and 1 km in the other areas. The tracks crossing the lines were counted 1–5 days after a snowfall.

The track index gives the number of crossings per 10 km and 24 h. We assumed a linear relationship between track indices and population densities (see also Högmander & Penttinen 1996).

Raccoon dog populations were monitored by our field assistants in southern Finland only, by using 'the scent station method' (Linhart & Knowlton 1975, Kauhala et al. 1999), because raccoon dogs hibernate and leave snow tracks only occasionally. Scent stations (50 per area) are patches of sand (radius about 1 m) with a stick in the middle that is dipped in gray fox *Urocyon cinereoargenteus* gland lure. When animals come and sniff the stick at night, they leave their foot prints in the sand. The stations were checked each morning during a 5-day period in early summer (late May-early June) in 1994–1998. The raccoon dog index gives the percentage of scent stations visited at least once during the 5-day period. I also tried to use this method for the mink, but mink tracks were too scarce to give a reliable index. Mink catch from the hunting season (August–April) was thus used as an index of mink abundance in the removal areas.

The number of breeding pairs of ducks were counted in May/early June upon arrival of migrating ducks. Pair counts were done on all water bodies in each study area, and birds were counted from the same sites each year. (Duck counts were not done in 1993 in eastern Finland because of the lack of field assistants). We included all species of dabbling and diving ducks observed in the study areas. Mallards *Anas platyrhynchos*, common teals *Anas crecca* and common goldeneyes *Bucephala clangula* were the most common species in southern and eastern Finland. Besides these, wigeons *Anas penelope*, northern pintails *Anas acuta* and tufted ducks *Aythya fuligula* were common in northern Finland. Two counts were done, as some ducks (mallards, teals, northern pintails, goldeneyes) arrive earlier than others (tufted ducks, wigeons) (Koskimies & Väisänen 1988). Two brood counts were done in late June and July to get a reliable estimate of the number of broods and ducklings produced in each area. The number of ducklings divided by the number of pairs gives the relative reproduction rate. All duck counts were performed by experienced field assistants.

### Statistical analyses

I used mainly nonparametric tests, because all variables were not normally distributed (Kolmogorov-Smirnov test). The statistical power of the tests is thus rather low. The trends in predator indices, the number of broods per pair and the relative reproduction rate (= ducklings/pair) were tested using Spearman rank correlation test (1-tailed). I used Wilcoxon signed rank test to examine the differences between the removal and control areas. I also compared the number of females with or without broods in the beginning and at the end of the study by using the $\chi^2$ -test. The relationships between predator indices and the relative reproduction rate of ducks was tested by using regression analysis. I smoothed the data by using 3-year moving averages to better reveal possible trends in the indices (Post & Stenseth 1999). The values for the first and last year were not smoothed. All analyses were performed with the software SYSTAT 10.

## Results

### Number of predators removed and trends in predator indices

In southern Finland, most predators removed (total N = 433) were raccoon dogs (280), but also some red foxes (49), pine martens (40) and American minks (64) (Table 1). No significant trends were observed in predator indices in southern Finland (Fig. 1). However,

in the removal area, the fox index first declined and then increased again towards the end of the study, while the raccoon dog index behaved in the opposite way, and there was negative correlation between these two indices (Rs = -0.90, $p<0.05$). Also fox and marten indices correlated negatively in the removal area (Rs = -1.00, $p<0.01$). The marten index declined at the beginning of the study in the control area.

In eastern Finland, most predators removed (total N = 186) were minks (88), but also many foxes (57) and martens (41) were caught. The fox index increased in the control area, as did the marten index towards the end of the study, but no significant trends in predator indices existed in the removal area (Fig. 1).

In northern Finland, most predators removed (total N = 132) were foxes (72), but also some martens (28) and minks (32) were caught. Both fox and marten indices declined in the removal area and increased in the control area (Fig. 1).

**Table 1.** Predator catches (ind./10 km$^2$) in the removal areas during the experiment, starting from the hunting season 1993/94. The hunting season is from 1 August to 30 April, except that of the pine marten, which is from 1 November to 31 March.

| Area | | 1993/94 | 1994/95 | 1995/96 | 1996/97 | 1997/98 |
|---|---|---|---|---|---|---|
| Southern Finland: | | | | | | |
| | R. dog | 7.6 | 12.2 | 13.6 | 10.2 | 7.3 |
| | Fox | 1.6 | 1.5 | 2.9 | 2.2 | 0.7 |
| | Marten | 1.6 | 1.1 | 2.2 | 2.0 | 0.4 |
| | Mink | 2.0 | 1.8 | 2.5 | 2.7 | 2.5 |
| Eastern Finland: | | | | | | |
| | Fox | 3.2 | 3.3 | 1.3 | 0.1 | - |
| | Marten | 2.9 | 1.3 | 1.1 | 0.4 | - |
| | Mink | 5.7 | 2.2 | 2.1 | 2.2 | - |
| Northern Finland: | | | | | | |
| | Fox | 2.4 | 1.4 | 2.0 | 1.4 | - |
| | Marten | 1.0 | 1.0 | 0.7 | 0.1 | - |
| | Mink | 1.0 | 0.8 | 0.6 | 0.8 | - |

## Breeding success of ducks

The numbers of breeding pairs of ducks are given in Fig. 2. In the spring of 1994, many new nest boxes for goldeneyes were taken to the removal area of southern Finland which resulted in an increase of breeding pairs of goldeneyes.

In southern Finland, the breeding success of diving ducks increased in the control area, whereas no significant trends in the breeding success of ducks could be seen in the removal area (Fig. 2). The number of broods per pair in the first and last year of the study period did not differ in either area (Table 2). The relative reproduction rate (ducklings/pair) of both dabbling and diving ducks was higher in the control area in southern Finland (Table 3).

In eastern Finland, the breeding success of ducks declined in both areas and was higher at the beginning of the study than at the end of it (Fig. 2, Table 2). There was no difference in the relative reproduction rate of ducks between removal and control areas in eastern Finland (Table 3).

In northern Finland, the breeding success of diving ducks improved in the removal area, whereas that of dabbling ducks declined in the control area (Fig. 2, Table 2). The breeding success of both dabbling and diving ducks was better in the removal area (Table 3).

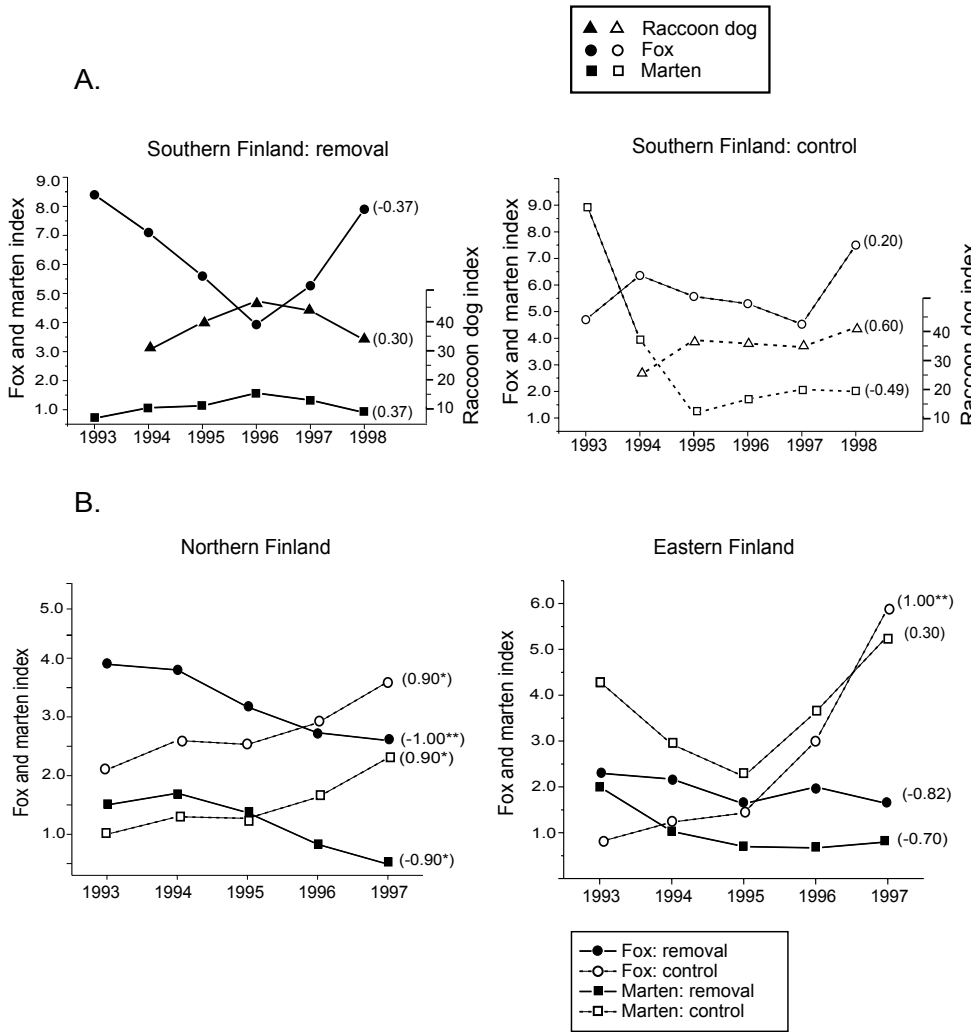


**Fig. 1.** Predator indices in southern Finland (A) and in northern and eastern Finland (B). Fox and marten indices give the number of snow tracks crossing the transect line per 10 km and 24 h. The raccoon dog index gives the percentage of scent stations visited during a 5-day period. Spearman rank correlation coefficients (Rs) are also given. One asterisk: $p<0.05$, two asterisks $p<0.01$ (one-sided test). Original figures of predator indices have been published in K a u h a l a et al. (1999).

The first prediction, that the breeding success of ducks will increase in predator removal areas and decrease in predator control areas, was proved only in northern Finland. The second prediction, that the effect of predator removal on duck breeding success will be greatest in southern Finland, did not hold.

## Predator indices and the breeding success of ducks

Since the breeding success of ducks declined sharply in both areas of eastern Finland (Fig. 2, Tables 2, 3), the treatment (predator removal/protection from hunting) did not seem to affect the breeding success of ducks. Therefore I excluded eastern Finland from the following analysis.

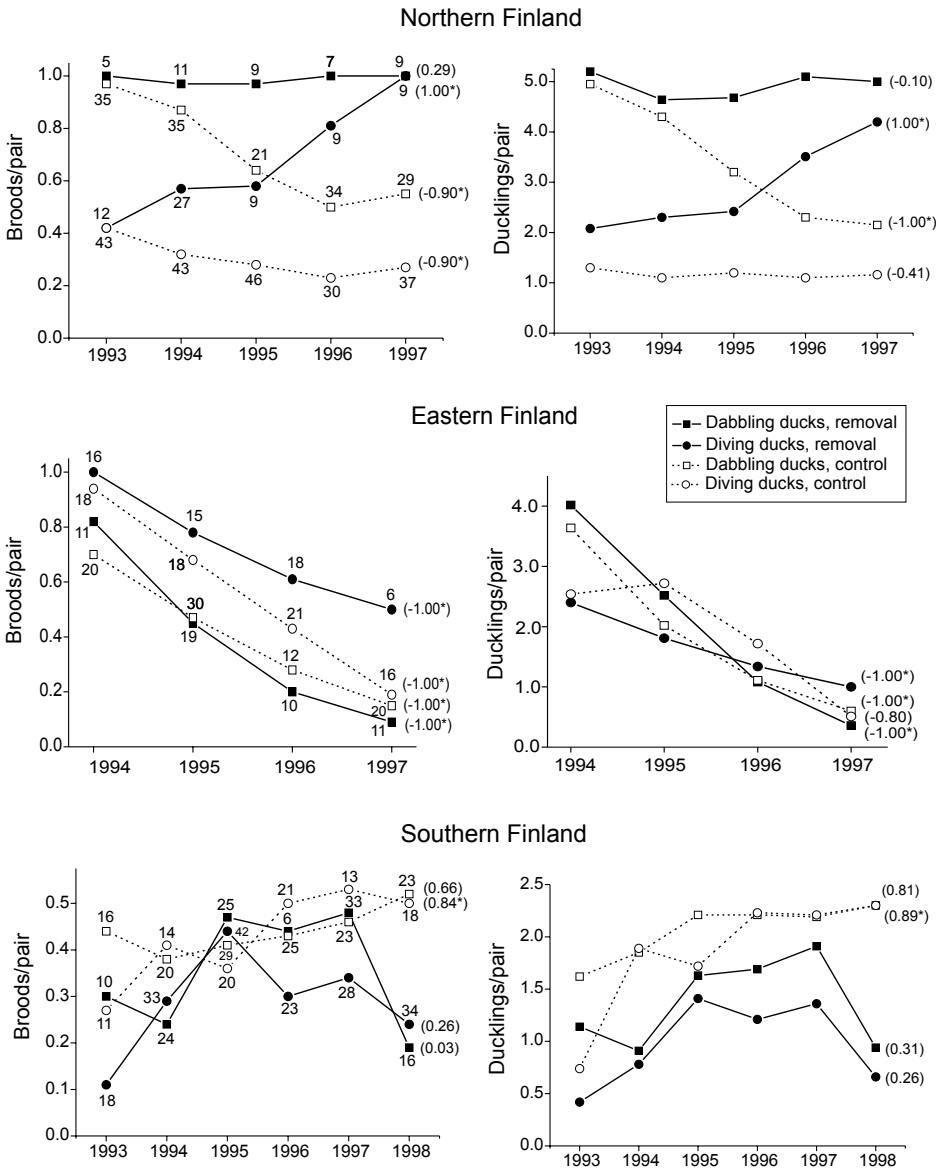


**Fig. 2.** The trends in the number of broods/pair and the relative reproduction rate of ducks (ducklings/pair) in predator removal and control areas in different regions of Finland. The number of pairs are given in the figure on the left. Spearman rank correlation coefficients (Rs) are also given. One asterisk: $p<0.05$, two asterisks $p<0.01$ (one-sided test).

In both areas of southern Finland, there was a positive relationship between the raccoon dog index and the relative reproduction rate of dabbling ducks, whereas the fox index correlated negatively with the breeding success of ducks in the removal area (Table 4). A negative relationship existed also between the marten index and the breeding success of ducks in the control area. The third prediction, that raccoon dog removal will increase breeding success of dabbling ducks in southern Finland, did thus not hold.

**Table 2.** Proportion of females with broods (broods/pair) compared between the first and last year of the study in each area using $\chi^2$-test. Df = 1 in each case. $\chi^2$-values are Yates-corrected when frequency in some cell is <5.

| Area/treatment | | Females with broods | | | |
|---|---|---|---|---|---|
| | | First year | Last year | $\chi^2$ | p |
| Southern Finland: | | | | | |
| Removal | Dabbling ducks | 0.30 | 0.19 | 0.03 | 0.854 |
| | Diving ducks | 0.11 | 0.24 | 0.24 | 0.477 |
| Control | Dabbling ducks | 0.44 | 0.52 | 0.27 | 0.605 |
| | Diving ducks | 0.27 | 0.50 | 0.67 | 0.228 |
| Eastern Finland: | | | | | |
| Removal | Dabbling ducks | 0.82 | 0.09 | 8.98 | 0.003 |
| | Diving ducks | 1.00 | 0.50 | 5.50 | 0.019 |
| Control | Dabbling ducks | 0.70 | 0.15 | 10.23 | 0.001 |
| | Diving ducks | 0.94 | 0.19 | 17.03 | < 0.001 |
| Northern Finland: | | | | | |
| Removal | Dabbling ducks | 1.00 | 1.00 | | NS |
| | Diving ducks | 0.42 | 1.0 | 5.45 | 0.019 |
| Control | Dabbling ducks | 0.97 | 0.55 | 13.98 | < 0.001 |
| | Diving ducks | 0.42 | 0.27 | 1.92 | 0.165 |

**Table 3.** Differences in reproductive parameters between removal and control areas, tested using the Wilcoxon Signed Rank test (two-sided).

| Area | | Broods/pair | | Ducklings/pair | |
|---|---|---|---|---|---|
| | | Z | p | Z | p |
| Southern Finland: | | | | | |
| | Dabbling ducks | 0.94 | 0.345 | 2.20 | 0.028 |
| | Diving ducks | 1.99 | 0.046 | 2.20 | 0.028 |
| Eastern Finland | | | | | |
| | Dabbling ducks | 0.37 | 0.715 | -0.73 | 0.465 |
| | Diving ducks | -1.83 | 0.068 | 0.73 | 0.465 |
| Northern Finland: | | | | | |
| | Dabbling ducks | -2.02 | 0.043 | -2.02 | 0.043 |
| | Diving ducks | -1.83 | 0.068 | -2.02 | 0.043 |

In the removal area of northern Finland there was a negative relationship between the fox and marten indices and the relative reproduction rate of diving ducks, whereas in the control area the relative reproduction rate of dabbling ducks correlated negatively with fox and marten indices. No significant correlation existed between the mink index (catch) and the breeding success of ducks in any area, although in northern Finland the relationship seemed to be negative (Table 4).

## Discussion

### The effect of predator removal on predator populations

Predator removal was most successful in northern Finland where study areas were large and predator densities rather low. In eastern Finland, the fox index increased in the control area, whereas predator indices slightly (but not significantly) decreased in the removal area during

**Table 4.** Relationship between predator indices and the relative reproduction rate of ducks (ducklings/pair) in predator removal and control areas, tested with regression analysis ($r^2$/F/p). NS = no model (p>0.01). Spearman Rank correlation coefficient, Rs, is also given (an asterisk indicates p<0.05, one-sided test).

| Area/treatment | | Fox | Marten | Raccoon dog | Mink |
|---|---|---|---|---|---|
| Southern Finland: | | | | | |
| Removal | Dabbling ducks | 0.69/8.7/0.042 | NS | 0.83/15.1/0.030 | NS |
| | | Rs = -0.71 | Rs = 0.71 | Rs = 0.90* | Rs = 0.62 |
| | Diving ducks | 0.77/13.3/0.022 | NS | NS | NS |
| | | Rs = -0.77 | Rs = 0.77 | Rs = 0.50 | Rs = -0.21 |
| Control | Dabbling ducks | NS | 0.88/28.9/0.006 | 0.96/79.9/0.003 | - |
| | | Rs = 0.52 | Rs = -0.81 | Rs = 0.98* | - |
| | Diving ducks | NS | 0.79/14.8/0.018 | NS | - |
| | | Rs = 0.37 | Rs = -0.37 | Rs = 0.40 | - |
| Northern Finland: | | | | | |
| Removal | Dabbling ducks | NS | NS | - | NS |
| | | Rs = 0.10 | Rs = -0.30 | - | Rs = -0.95 |
| | Diving ducks | 0.83/15.0/0.030 | 0.94/48.5/0.006 | - | NS |
| | | Rs = -1.00* | Rs = -0.90* | - | Rs = -0.63 |
| Control | Dabbling ducks | 0.73/7.9/0.067 | 0.70/7.0/0.078 | - | - |
| | | Rs = -0.90* | Rs = -0.90* | - | - |
| | Diving ducks | NS | NS | - | - |
| | | Rs = -0.67 | Rs = -0.67 | - | - |

the experiment. Especially at the end of the study predator densities thus differed between the removal and control areas, pointing to the conclusion that predator removal was rather successful also in eastern Finland.

In southern Finland, the effect of predator removal on predator abundance was not so evident. Although 280 raccoon dogs were caught from the removal area, no significant decrease in the raccoon dog index was observed. One reason behind this may be the fact that most raccoon dogs were caught in autumn and were juveniles that would have died anyway. Some juveniles may also have immigrated to the removal area from neighbouring areas, because juveniles may disperse far (Kauhala & Helle 1994). Furthermore, like other canids, raccoon dogs also tend to increase their litter size under high hunting pressure and thus counteract – and even overcompensate – removal (K. Kauhala, unpublished data).

In the removal area of southern Finland, the fox index first declined but then increased again at the end of the study, indicating that fox removal was not very effective towards the end of the study. Because fox and raccoon dog indices correlated negatively, it is possible that there is competition between these species and, if the hunting pressure towards one of the them is high, the other one may benefit and increase in numbers. Competition is likely, because foxes and raccoon dogs share a large part of their diet (Kauhala et al. 1998). Intraguild predation (foxes killing raccoon dogs) is unlikely, because raccoon dogs do not seem to avoid foxes (Kauhala et al., unpublished data). A negative relationship between fox and raccoon dog numbers has also been observed in Germany in recent years (Schwarz et al. 2002). Indeed, intraguild aggression between different canid species is common (Macdonald & Sillero-Zubiri 2004).

Marten removal in southern Finland had no obvious effect on the marten index, but marten numbers were low even in the beginning of the experiment. There was also a negative

relationship between fox and marten indices in the removal area, maybe due to intraguild predation, as was suggested by Lindström et al. (1995). The marten index crashed in the control area in the beginning of the study, probably because vole numbers peaked in 1992 and declined and remained low thereafter (Kauhala et al. 1999). The vole index (voles trapped per 100 trap-nights) was 25.8 in 1992 and 1.1–4.7 in 1993–1998.

### Impact of predators on the breeding success of ducks

In northern Finland, different treatments resulted in different trends in the breeding success of ducks. The results of the present study from northern Finland are similar to those of many North American studies. Balser et al. (1968), Duebbert & Kantrud (1974), Duebbert & Lokemoen (1980), Lokemoen & Woodward (1993) and Garrettson & Rohwer (2001) found that removal of mammalian predators dramatically increased duck nest success. LaGrange et al. (1995) noticed that nest success of dabbling ducks was greater inside an enclosure, which prevented medium-sized carnivores from entering, than outside the enclosure. Also Lokemoen et al. (1982), Greenwood et al. (1990) and Cowardin et al. (1998) reported high breeding success of ducks in enclosures.

Both fox and marten numbers seemed to affect the breeding success of especially diving ducks in northern Finland. Martens may destroy the nests of e.g. goldeneyes. Also in other studies martens were found to be the primary nest predators of goldeneyes in Finland (Pöysä et al. 1997). Martens and foxes may also prey on ducklings of both dabblers and divers, when these are on their way from the nest to the water body. During these sometimes rather long walks ducklings may be very vulnerable to predation by mammalian predators. Foxes may also destroy the nests or kill the females of dabbling ducks. The red fox was found to be an important predator of duck nests and females also in North America (Sargeant 1972, Johnson & Sargeant 1977, Johnson et al. 1989, Fleskes & Klaas 1993, Sovada et al. 1995, Garrettson et al. 1996) and coastal birds in Germany (Helbig & Klenke 1995, according to Bellebaum 2002).

Predator (mainly raccoon dog) removal did not result in better breeding success of ducks in southern Finland. Either predator removal was not successful enough or raccoon dogs do not have a noteworthy effect on the breeding success of waterfowl. The positive correlation between the raccoon dog index and the breeding success of dabbling ducks suggests that the latter alternative is true. It is also possible that the number of other predators, especially the fox, removed was too low; other studies have shown that removal of only one predator or part of a diverse community of predators does not lead to an increase in the breeding success of game birds (Balser et al. 1968, Greenwood 1986, Clark et al. 1995). Functional responses of other predators including avian predators like crows *Corvus corone* or goshawks *Accipiter gentilis*, may be involved, and the overall effect of predator removal may thus be neutral. Manipulations may have complex impacts on predator communities (Paine et al. 1990), and removing mainly one predator species may also result in a numerical response from other predators, leading to compensatory predation (Goodrich & Buskirk 1995, Palomares et al. 1995, Sovada et al. 1995, Dion et al. 1999). The negative relationship between the fox and raccoon dog indices in the removal area supports this idea. Furthermore, in early summer birds occur more frequently in fox diet than in raccoon dog diet in southern Finland (Kauhala et al. 1998).

The fox may thus be the major predator of dabbling duck nests and broods in southern Finland. Fox density is high in southern Finland, and foxes may prey both on eggs and incubating females such as mallards (Sargeant 1972, Fleskes & Klaas 1993), whereas raccoon dogs consume only eggs but do not usually catch females (O. Opermanis, in litt.). Thus, mallards may lay a new clutch, if the first one is destroyed by a raccoon dog. But if the fox finds the nest, no renesting can occur if the female is killed. Furthermore, raccoon dogs spend much time on shores in early summer (Kauhala 1996), whereas mallards and teals usually nest in the forest. The habit of nesting in the forest may have evolved as an adaptation to the presence of mustelid predators, like the European mink *Mustela lutreola* that lives near water (now extinct in Finland). In Latvia, of 1059 duck nests destroyed by predators on an eutrophic wetland, only 0.6% were attributed to raccoon dogs (Opermanis et al. 2001). This also points to the conclusion that the impact of raccoon dogs on duckling production is of minor importance.

The increase in the breeding success of diving ducks in the control area of southern Finland may be due to the decline in the marten population after the crash in vole numbers. The mink index did not explain the variation in the breeding success of ducks in any area. However, in northern Finland, there was a negative (but not significant) relationship between the mink index and the breeding success of ducks. Thus, the mink may have some effect in the north, but more evidence and a better index for mink abundance is needed.

In eastern Finland, the breeding success of ducks declined sharply in both areas, suggesting that other factors than mammalian predators were involved. Beauchamp et al. (1996) also found that nest success in removal and unmanaged sites did not differ (58 studies reviewed in the prairies) and nest success declined over time at similar rates both at sites with and without predator management. Thus, nest loss due to mammalian predators did not appear to be the cause of the long-term decline in nest success in the prairie region. The results of predator removal studies thus differ between areas according to the local circumstances.

## Conclusions

1) Where predator numbers are rather low and areas large, as in northern Finland, fox and marten removal may have considerable effect on predator numbers and the breeding success of ducks.
2) The study gave no evidence that the introduced raccoon dog has a negative impact on the breeding success of dabbling ducks. Instead, foxes and martens seemed to be more important predators of duck nests and broods also in southern Finland.
3) Removing mainly one predator, like the raccoon dog, may not have the desired effect on the breeding success of birds, because both the numeric and functional response of other predators, like the fox, may increase and lead to compensatory predation.
4) The effect of the American mink on duckling production could not be verified in this study, and further research on this subject is needed.

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## LITERATURE


BALL I.J., ENG R.L. & KRAFT BALL S. 1995: Population density and productivity of ducks on large grassland tracts in northcentral Montana. *Wildl. Soc. Bull. 23: 767–773.*

BALSER D.S., DILL H.H. & NELSON H.K. 1968: Effect of predator reduction on waterfowl nesting success. *J. Wildl. Manage. 32: 669–682.*

BARTOSZEWICZ M. & ZALEWSKI A. 2003: American mink, *Mustela vison* diet and predation on waterfowl in the Słońsk Reserve, western Poland. *Folia Zool. 52: 225–238.*

BEAUCHAMP W.D., NUDDS T.D. & CLARK R.G. 1996: Duck nest success declines with and without predator management. *J. Wildl. Manage. 60: 258–264.*

BELLEBAUM J. 2002: Prädation als Gefährdung bodenbrütender Vögel in Deutschland – Eine Übersicht. *Ber. Vogelschutz 39: 95–117.*

CLARK R.G., MEGER D.E. & IGNATIUK J.B. 1995: Removing American crows and duck nesting success. *Can. J. Zool. 73: 518–522.*

CÔTÉ I.M. & SUTHERLAND W.J. 1997: The effectiveness of removing predators to protect bird populations. *Cons. Biol. 11: 395–405.*

COWARDIN L.M., GILMER D.S. & SHAIFFER C.W. 1985: Mallard recruitment in the agricultural environment of North Dakota. *Wildl. Monogr. 92: 1–37.*

COWARDIN L.M., PIETZ P.J., LOKEMOEN J.T., SKLEBAR H.T. & SARGEANT G.A. 1998: Response of nesting ducks to predator exclosures and water conditions during drought. *J. Wildl. Manage. 62: 152–163.*

DION N., HOBSON K.A. & LARIVIÈRE S. 1999: Effects of removing duck-nest predators on nesting success of grassland songbirds. *Can. J. Zool. 77: 1801–1806.*

DUEBBERT H.F. & KANTRUD H.A. 1974: Upland duck nesting related to land use and predator reduction. *J. Wildl. Manage. 38: 257–265.*

DUEBBERT H.F. & LOKEMOEN J.T. 1980: High duck nesting success in a predator-reduced environment. *J. Wildl. Manage. 44: 428–437.*

EBENHARD T. 1988: Introduced birds and mammals and their ecological effects. *Swedish Wildl. Res. 13: 1–107.*

FERRERAS P. & MACDONALD D.W. 1999: The impact of American mink *Mustela vison* on water birds in the upper Thames. *J. Appl. Ecol. 36: 701–708.*

FLESKES J. P. & KLAAS E.E. 1993: Remains of ducks and other prey found near fox and mink dens on an Iowa wildlife refuge. *Prairie Naturalist 25: 43–50.*

GARRETTSON P.R. & ROHWER F.C. 2001: Effects of mammalian predator removal on production of upland-nesting ducks in North Dakota. *J. Wildl. Manage. 65: 398–405.*

GARRETTSON P.R., ROHWER F.C & ZIMMER J.M. 1996: Effects of mammalian predator removal on waterfowl and non-game birds in North Dakota. *Trans. N. Am. Wildl. Nat. Resour. Conf. 61: 94–101.*

GOODRICH J.M. & BUSKIRK S.W. 1995: Control of abundant native vertebrates for conservation of endangered species. *Cons. Biol. 9: 1357–1364.*

GREENWOOD R.J. 1986: Influence of striped skunk removal on upland duck nest success in North Dakota. *Wildl. Soc. Bull. 14: 6–11.*

GREENWOOD R.J., ARNOLD P.M. & MCGUIRE B.G. 1990: Protecting duck nests from mammalian predators with fences and a toxicant. *Wildl. Soc. Bull. 18: 75–82.*

GREENWOOD R.J., SARGEANT A.B., JOHNSON D.H., COWARDIN L.M. & SHAFFER T.L. 1995: Factors associated with duck nest success in the prairie pothole region of Canada. *Wildl. Monogr. 128: 1–57.*

HELBIG A.J. & KLENKE R. 1995: Wirksamkeit von Schutzgebieten für die Bestandserhaltung gefährdeter Küstenvögel in Abhängigkeit vom Einfluß tierischer Räuber. *Abschlußbericht an das Umweltministerium Mecklenburg-Vorpommern, Kloster.*

HÖGMANDER H. & PENTTINEN A. 1996: Some statistical aspects of Finnish wildlife triangles. *Finnish Game Res. 49: 37–43.*

JOHNSON D.H. & SARGEANT A.B. 1977: Impact of red fox predation on the sex ratio of prairie mallards. *U.S. Fish and Wildllife Service. Wildl. Res. Rep. 6: 1–56.*

JOHNSON D.H., SARGEANT A.B. & GREENWOOD R.J. 1989: Importance of individual species of predators on nesting success in the Canadian prairie pothole region. *Can. J. Zool. 67: 291–297.*

KAUHALA K. 1996: Habitat use of raccoon dogs, *Nyctereutes procyonoides*, in southern Finland. *Z. Säugetierk. 61: 269–275.*

KAUHALA K. & HELLE E. 1994: Supikoiran elinpiireistä ja yksiavioisuudesta Etelä-Suomessa (Home ranges and monogamy of the raccoon dog in southern Finland). *Suomen Riista 40: 32–41 (in Finnish with English summary).*

KAUHALA K., LAUKKANEN P. & VON RÉGE I. 1998: Summer food composition and food niche overlap of the raccoon dog, red fox and badger in Finland. *Ecography 21: 457–463*.
KAUHALA K., HELLE P., HELLE E. & KORHONEN J. 1999: Impact of predator removal on predator and mountain hare populations in Finland. *Ann. Zool. Fennici 36: 139–148*.
KAUHALA K., HELLE P. & HELLE E. 2000: Predator control and the density and reproductive success of grouse populations in Finland. *Ecography 23: 161–168*.
KLETT A.T., SHAFFER T.L. & JOHNSON D.H. 1988: Duck nest success in the prairie pothole region. *J. Wildl. Manage. 52: 431–440*.
KOSKIMIES P. & VÄISÄNEN R. 1988: Linnustonseurannan havainnointiohjeet (Monitoring bird populations in Finland: a manual). *Helsingin yliopiston eläinmuseo (in Finnish with English summary)*.
LAGRANGE T.G., HANSEN J.L., ANDREWS R.D., HANCOCK A.W & KIENZLER J.M. 1995: Electric fence predator exclosure to enhance duck nesting: a long-term case study in Iowa. *Wildl. Soc. Bull. 23: 261–266*.
LINDÉN H., HELLE E., HELLE P. & WIKMAN M. 1996: Wildlife triangle scheme in Finland: methods and aims for monitoring wildlife populations. *Finnish Game Res. 49: 4–11*.
LINDSTRÖM E.R., BRAINERD S.M., HELLDIN J.O. & OVERSKAUG K. 1995: Pine marten – red fox interactions: a case of intraguild predation? *Ann. Zool. Fennici 32: 123–130*.
LINHART S.B. & KNOWLTON F.F. 1975: Determining the relative abundance of coyotes by scent station lines. *Wildl. Soc. Bull. 3: 119–124*.
LOKEMOEN J.T. & WOODWARD R.O. 1993: An assesment of predator barriers and predator control to enhance duck nest success on peninsulas. *Wildl. Soc. Bull. 21: 275–282*.
LOKEMOEN J.T., DOTY H.A., SHARP D.E. & NEAVILLE J.E. 1982: Electric fences to reduce mammalian predation on waterfowl nests. *Wildl. Soc. Bull. 10: 318–323*.
MACDONALD D.W. & SILLERO-ZUBIRI C. 2004: Dramatis personae. Wild canids – an introduction and dramatis personae. In: Macdonald D.W. & Sillero-Zubiri C. (eds), Biology and conservation of wild canids. *Oxford University Press, Oxford: 3–36*.
MAXSON S.J. & RIGGS M.R. 1996: Habitat use and nest success of overwater nesting ducks in westcentral Minnesota. *J. Wildl. Manage. 60: 108–119*.
NORDSTRÖM M., HÖGMANDER J., NUMMELIN J., LAINE J., LAANETU N. & KORPIMÄKI E. 2002: Variable responses of waterfowl breeding populations to long-term removal of introduced American mink. *Ecography 25: 385–394*.
NORDSTRÖM M., HÖGMANDER J., NUMMELIN J., LAINE J., LAANETU N. & KORPIMÄKI E. 2003: Effects of feral mink removal on seabirds, waders and passerines on small islands in the Baltic Sea. *Biol. Cons. 109: 359–368*.
OPERMANIS O., MEDNIS A. & BAUGA I. 2001: Duck nests and predators: interaction, specialisation and possible management. *Wildl. Biol. 7: 87–96*.
PAINE R.T., WOOTTON J.T. & BOERSMA P.D. 1990: Direct and indirect effects of peregrine falcon predation on seabird abundance. *Auk 107: 1–9*.
PALOMARES F., GAONA P., FERRERAS P. & DELIBES M. 1995: Positive effects on game species of top predators by controlling smaller predator populations: an example with lynx, mongooses, and rabbits. *Cons. Biol. 9: 295–305*.
POST E. & STENSETH N.C. 1999: Climatic variability, plant phenology, and northern ungulates. *Ecology 80: 1322–1339*.
PÖYSÄ H., MILONOFF M. & VIRTANEN J. 1997: Nest predation in hole-nesting birds in relation to habitat edge: an experiment. *Ecography 20: 329–335*.
SARGEANT A.B. 1972: Red fox spatial characteristics in relation to waterfowl predation. *J. Wildl. Manage. 36: 225–236*.
SARGEANT A.B., SOVADA M.A. & SHAFFER T.L. 1995: Seasonal predator removal relative to hatch rate of duck nests in waterfowl production areas. *Wildl. Soc. Bull. 23: 507–513*.
SCHWARZ S., SUTOR A. & LITZBARSKI H. 2002: Nachweise des Marderhundes (*Nyctereutes procyonoides*) im Europäischen Vogelschutzbebiet (SPA) Havelländisches Luch. *Naturschutz und Landschaftspflege in Brandenburg 11: 198–199*.
SOVADA M.A., SARGEANT A.B. & GRIER J.W. 1995: Differential effects of coyotes and red foxes on duck nest success. *J. Wildl. Manage. 59: 1–9*.