Balancing between predation risk and food by boreal breeding ducks

Sari Holopainen[1], Elmo Miettinen[1], Veli-Matti Väänänen[1], Petri Nummi[1], and Hannu Pöysä[2]

[1]University of Helsinki
[2]University of Eastern Finland

June 13, 2023

Abstract

1. Wetlands belong to the globally most threatened habitats, and organisms depending on them are of conservation concern. Wetland destruction and quality loss may affect negatively also boreal breeding ducks in which habitat selection often needs balancing between important determinants of habitat suitability. In Finland duck population trajectories are habitat-specific, while the reasons behind are not known. 2. In this research, the balance of nest predation risk and invertebrate food abundance in boreal breeding ducks was studied in Finland at 45 lakes and ponds in 2017 and 2018. Nest predation experiments were conducted with artificial nests followed by wildlife cameras during seven days. Invertebrates were sampled from the study water bodies using emergence and activity traps. Duck pairs and broods were also surveyed from these and 18 additional water bodies. 3. The wildlife camera results indicate that predation risk was higher in the water bodies surrounded by agricultural land than forestland. Ponds (seasonal, beaver and man-made) had lower nest predation risk and they were also more invertebrate-rich habitats than permanent lakes. In addition, artificial nests further away from water bodies had higher survival than shoreline nests. Habitat use of duck pairs (prior to nesting) was not associated with invertebrate food, but duck broods preferred habitats rich in food. 4. High nest predation pressure in shorelines of especially agricultural landscapes may contribute the declining population trends of ducks in Finland. Controlling predators would be an important conservation action to improve duck breeding success. This research underlines the benefits of the availability of different water body types for the breeding ducks. There is an urgent need to pay attention to protecting seasonal ponds, while the lack of flooded waters may be mitigated by favouring beavers or man-made ponds.

Balancing between predation risk and food by boreal breeding ducks

Sari Holopainen [1], Elmo Miettinen[2], Veli-Matti Väänänen [1], Petri Nummi[1]and Hannu Pöysä[3]

1. Department of Forest Sciences, P.O. Box 27, University of Helsinki, FI-00014 Helsinki, Finland. e-mail: sari.holopainen@helsinki.fi. Phone : +358-504489538. Orcid: 0000-0002-3271-4468

2. Organismal and Evolutionary Biology Research Programme, Faculty of Biological and Environmental Sciences, P.O.Box 62, University of Helsinki, FI-00014 Helsinki, Finland. Orcid: 0000-0002-5354-7531

3. University of Eastern Finland, Department of Environmental and Biological Sciences, POB 111, FI-80101 Joensuu, Finland.

Key words

Alien predator, invertebrate, nest predation, waterbird, wetland, wildlife camera

Abstract

1. Wetlands belong to the globally most threatened habitats, and organisms depending on them are of conservation concern. Wetland destruction and quality loss may affect negatively also boreal breeding ducks in which habitat selection often needs balancing between important determinants of habitat suitability. In Finland duck population trajectories are habitat-specific, while the reasons behind are not known.

2. In this research, the balance of nest predation risk and invertebrate food abundance in boreal breeding ducks was studied in Finland at 45 lakes and ponds in 2017 and 2018. Nest predation experiments were conducted with artificial nests followed by wildlife cameras during seven days. Invertebrates were sampled from the study water bodies using emergence and activity traps. Duck pairs and broods were also surveyed from these and 18 additional water bodies.

3. The wildlife camera results indicate that predation risk was higher in the water bodies surrounded by agricultural land than forestland. Ponds (seasonal, beaver and man-made) had lower nest predation risk and they were also more invertebrate-rich habitats than permanent lakes. In addition, artificial nests further away from water bodies had higher survival than shoreline nests. Habitat use of duck pairs (prior to nesting) was not associated with invertebrate food, but duck broods preferred habitats rich in food.

4. High nest predation pressure in shorelines of especially agricultural landscapes may contribute the declining population trends of ducks in Finland. Controlling predators would be an important conservation action to improve duck breeding success. This research underlines the benefits of the availability of different water body types for the breeding ducks. There is an urgent need to pay attention to protecting seasonal ponds, while the lack of flooded waters may be mitigated by favouring beavers or man-made ponds.

Cover letter

Dear Editors,

we submit the MS "Balancing between predation risk and food by boreal breeding ducks" for publication in the special issue of Ecology and Evolution "Ecological Insights from Camera Trapping".

We studied the effects of wetland quality for boreal breeding ducks from the two important aspects: predation and food. We used wildlife cameras for reliable nest predator identification around different breeding habitats of ducks. Interestingly, we did find that duck food availability is low and nest predation pressure is high at permanent lakes, while ponds (seasonal, beaver, man-made) were shown to be food rich habitats with low nest predation pressure. However, ponds are commonly not protected and for example seasonal ponds are typically drained for farmland or to improve forest grow. Our results emphasize the benefits of different wetland types in the landscape for the breeding ducks. Even important bird lakes might have high predation pressure, which underlines the need of predator control, especially concerning alien species. We think that our manuscript is timely and offer much needed information about conservation of wetland ecosystems from aspects that are so far poorly covered. Wildlife cameras turned out really useful method for identifying different predator species, even they took the eggs without leaving any clues behind.

Sincerely, on behalf of the authors,

Sari Holopainen

INTRODUCTION

Humans have altered wetland ecosystems in numerous ways across the globe, especially through drainage for agricultural land (Davidson, 2014; Gibbs, 2000; Hu et al., 2017; Kingsford et al., 2016). In boreal forest areas, peatlands and other riparian forest habitats have been ditched to increase wood production (Kuusisto et al., 1998). In addition to direct wetland destruction, climate warming (McMenamin et al.,2008) and over-exploitation of wetland creating beavers (Halley et al. 2021) have had an indirect effect on the amount and distribution of wetlands. Furthermore, wetland quality is threatened for instance due to eutrophication and alien species introductions (Fox et al., 2019; Ramsar Convention Secretariat 2010; Ma et al., 2010;

Guillemain et al.,2013; Nummi et al., 2019a). All in all, human-induced environmental wetland change has therefore impacted aquatic animals at multiple levels of organization from individuals to landscapes (Sievers et al., 2018).

Habitat characteristics are important determinants of breeding densities and production of ducks on boreal wetlands (Holopainen et al.,2015). Many boreal lakes lack the habitat structure and sufficient food resources to support breeding ducks, making them unsuitable for brood rearing (Sjöberg et al., 2000). Indeed, duckling mortality at lakes with limited food resources, in particular invertebrates, is high (Gunnarsson et al., 2004; Nummi & Hahtola, 2008). In spring, however, patterns of snowmelt create annual variation in the nature and extent of shallow flooded lakeshores affecting littoral ecosystem productivity (Larmola et al., 2004). Seasonal floods and ponds that commonly dry during the summer offer important food-rich habitats for ducks (Holopainen et al., 2014), despite their highly variable occurrence. In addition, habitat engineering by beavers (*Castor* spp.) modifies oligotrophic, sharp-edged boreal lakes into productive shallow wetlands with ambiguous shorelines. Both beaver ponds and seasonal ponds typically have varying shorelines and possibly no fish or low fish densities (Nummi & Hahtola, 2008).

Habitat selection of breeding ducks is not straight-forward, but will possibly lead to trade-off situations, both between and within different stages of the breeding season. For example, experimental data by Gunnarsson and Elmberg (2008) suggests a trade-off between wetland use and nest survival in forested versus agricultural landscapes in the mallard (*Anas platyrhynchos*); wild waterfowl, including mallard, seemed to prefer agricultural landscape, while facing higher nest predation risk there. While predation risk largely determines nest site use and nesting success, food resources and habitat structure are the key characteristics affecting habitat use by duck pairs and broods as well as subsequent breeding success in boreal lakes (Holopainen et al., 2015). At wetlands, complex habitat structure and luxuriant vegetation are linked, as the abundance of emergent vegetation typically increases from nutrient-poor oligotrophic to nutrient-rich eutrophic lakes (Kauppinen & Väisänen, 1993; Holopainen & Lehikoinen, 2021).

Changes in important boreal environmental characteristics may already have affected breeding ducks negatively. Finnish national duck pair surveys show declining trends for several species, but those breeding in eutrophic lakes have declined more than in oligotrophic lakes (Lehikoinen et al., 2016; Pöysä et al., 2013). In addition to detrimental effects of over-growth of eutrophic waters, disproportionally increased predator pressure is one of the suspected reasons for the differences in population trajectories between habitats and also between species within habitats (see Pöysä et al., 2019; Pöysä & Linkola 2021), potentially impacting flyway-level trends in population size and structure (e.g. Brides et al., 2017). Indeed, artificial duck nest experiments with wildlife cameras in northern Europe have shown that nest predation rate is high especially around wetlands and in agricultural landscape, where also alien mammal species now occur (Holopainen et al., 2020a). As a result, duck species nesting on eutrophic lakes and especially those preferring shorelines as nesting places have, in all likelihood, experienced a major increase in predator diversity and abundance, which may have contributed to their declining population trends (Holopainen et al., 2021; Pöysä & Linkola, 2021).

In this article the complex habitat-based associations with ducks breeding success will be analysed. We will assess whether and how habitat selection and brood production by boreal breeding ducks result from a trade-off between nest predation risk and food availability. Specifically, wildlife cameras were used at artificial nests (mimicking dabbling duck nests) to measure nest predation risk at both the local habitat (shoreline nests versus forest nests) and landscape (proportion of agricultural land versus forest in the landscape) scales. Next, habitat selection of both breeding pairs and broods were assessed emphasising the role of landscape and food availability (invertebrate abundance). In addition, brood production at the landscape scale was measured. The hypothesis is that while eutrophic wetlands in agricultural landscapes typically produce more invertebrates, they will also have a higher nest predation rate and thus lower brood production. Furthermore, contrary to permanent lakes, it is expected that flooded ponds offer the most food-rich brood habitats but also safe nesting places.

METHODS

2.1 Study areas

For this study, water bodies surrounded with different proportions of forest versus agricultural land were selected: different landscapes to cover the whole gradient from fully forested to mainly agricultural were chosen. Landscape might affect not only the lake trophic status, but also the nest predator community, as stated by Holopainen et al. (2020a). Studies were conducted at lakes and ponds at two areas in Finland, Evo and Maaninka (Figure 1). Both areas have permanent lakes, which carry water through the summer. Lake shorelines may be affected by spring floods, but otherwise the water level is rather constant. The trophic level among these lakes vary from oligotrophic to eutrophic (see Holopainen & Lehikoinen, 2021). In addition to permanent lakes, in both areas the study included other wetlands, which were shallow and had temporally varying shorelines: seasonal ponds, beaver ponds and man-made ponds (hereafter ponds). Hereafter all lakes and ponds are called water bodies. The same mammalian predators and all common corvid species occur in both study areas (Lindén et al., 1996; Valkama et al., 2011).

Evo in southern Finland (61°12'N, 25°07'E) represents a typical boreal forest landscape in Finland. Human settlements are scarce, with few agricultural fields (hereafter fields) inside the study area and larger agricultural lands south from the studied water bodies. The lands within 1 km of the Evo water bodies consists on average 1 % of fields (range 0–6%).

In Evo duck surveys were undertaken at 45 water bodies (27 permanent lakes, 10 beaver ponds and 8 seasonal ponds) within a c. 39-km^2 area. Water body size varied between 0.04–37 ha. The median shoreline length for permanent lakes was 1.0 km and for ponds 0.5 km. From the 45 study water bodies, six seasonal, six beaver ponds and 12 permanent lakes were chosen for nest predation experiments and invertebrate surveys (for more information, see Supplementary Appendix S1).

Maaninka in eastern Finland (63@15'N, 27@30'E) is a mosaic of agricultural land and forests with some internationally important bird-lakes (Natura 2000 and IBA -lakes; Leivo et al., 2002). The area represents typical agricultural landscape of Finnish lake district. Duck surveys were made at 18 lakes and seasonal ponds across c. 47 km^2: 17 water bodies were used for the experiments, among them the important bird-lakes. All seasonal ponds were included that occurred during the study years and to which permission was granted from the landowners. The lands within 1 km of the water bodies consists on average 59% of fields (range 24–75%), the remainder mainly private forest. Water body sizes were 1–149 ha. The median shoreline length for permanent lakes was 3.0 km and for ponds 1.1 km. In total there were seven permanent lakes, two man-made ponds and eight seasonal ponds for nest experiments and invertebrate surveys.

To estimate the landscape structure (i.e. the field percentage) near the study water bodies, QGIS 2.18.7 (QGIS Development Team, 2017) and topographic vector map (National Land Survey of Finland, 03/2019) were used. The 1 km radius zones around the water bodies were measured from the shoreline. We used the 1km radius, as in the comparisons of nest predation patterns between 500 m and 250 m radius zones, the 250 m zone has shown to have habitat specific effects, while the effects disappear with a larger zone (Uusihakala, 2021). Thus we believe that 1 km radius zone describes the landscape scale foraging range of mammals. Waters from the zones were excluded in order to count the field percentage of surrounding land areas.

2.2 Artificial nest survival experiment with wildlife cameras

Artificial nest experiments were conducted in 2017 and 2018 to study nest predation rates at the water bodies. Nests were placed in sites where a dabbling duck hen could possibly lay a clutch, based on our own experience (nest site selection of boreal ducks is poorly studied, review by Holopainen et al., 2015; see also Väänänen et al., 2016). Some dabbling duck species nest at the shoreline, while others can place nests in the forest far from water bodies, so the artificial nest sites reflected this distribution. Each nest contained two farmed mallard eggs and some down from shot mallard females, mimicking the situation in the early stage of egg laying. Nests were constructed to resemble real ones: natural nest material from the nest surroundings was collected to form c. 20 cm wide nest cup and cover the eggs lightly. Eggs were not covered with down since ducks do not typically cover them before starting incubation. Nests were set under small trees or bushes, so they were hardly detectable from above. In open areas nests were established within tussocks.

Experimental nests were established in pairs around the water bodies: shoreline nests were placed less than five metres from shorelines and forest nests at least 70 metres from the shoreline nest (for more information, see Supplementary Appendix S2). In 2017 there were 46 nests at Evo and 42 at Maaninka, and in 2018 the numbers were 48 and 42, respectively (in total 178 nests). Density of the experimental nests was c. 1.2 nest/km² at Evo and 0.9 nests/km² at Maaninka. At Evo, every water bodies had only one nest pair a year, while at Maaninka there were fewer, but larger water bodies, and thus 2–3 nest pairs around the water bodies were established if possible. The same nest sites were used in both years to minimize the site effect.

Wildlife cameras (20 Uovision UV595-Full HD 12MP and four Niteforce Professional Trail Camera 12 MP) were set at artificial nests to identify predator nest visits and depredation time. Light-triggered passive wildlife cameras were ca. 1–1.5 m from nests, attached on trees or 1 m stakes. Cameras were active the whole seven day period responding to movement and were adjusted to take three pictures in a row, followed by a one-minute pause. The nest experiment was started during the pair survey (see 2.3 Duck and invertebrate surveys), the time when ducks initiate egg laying. One nest experiment round took seven days, and all the nests of a round were established and deconstructed on the same day between 9 am and 16 pm. Two rounds of nest experiments with different set of water bodies were carried out on each study area (i.e. two one-week experiments with 20–24 nests at the time). Nests were not visited by researchers during the seven-day exposure period.

2.3 Duck and invertebrate surveys

The duck species studied here are ground nesting and distributed widely in the boreal zone: mallard, common teal (*Anas crecca;* hereafter teal), Eurasian wigeon (*Mareca penelope*), northern pintail (*Anas acuta*), northern shoveler (*Spatula clypeata*), garganey (*S. querquedula*) and tufted duck (*Aythya fuligula*). All bred in Maaninka, but only the first two species bred at Evo. Duck pair and brood surveys were made in 2017 and 2018 with standard waterbird round count methods (Koskimies & Väisänen, 1991). In the round count the wetlands were surveyed by moving around the lake by a boat, stand up paddling board or by foot near the shoreline so that all the settled birds were detected with a high probability. Pair surveys were conducted in April and May right after the ice melt, when duck pairs occupy their breeding wetlands and are preparing for nesting. Ice melting sets an exact time frame for the duck surveys (Pöysä, 1996, 2019), making it possible to calibrate the phenology between different areas and years. Pairs and lone males were considered as pairs. Also groups of 2–4 males were used to estimate the number of pairs (i.e., 2–4 pairs). If the number of females surpassed the number of males at a wetland, the number of females was used instead. Brood surveys were conducted twice a year in the early June and July. The species, number and age of ducklings were recorded for each brood (Pirkola & Högmander, 1974). When studying brood habitat use, all brood observations were used for the analyses to determine the diverging habitat use of different age classes (i.e. some broods might occur twice in the analyses). When analysing brood production, every brood was identified based on their age and count, thus counting each brood only once.

Invertebrate trapping was conducted in the water bodies in June 2017 and 2018 during the first brood survey. All details of the trapping procedure were identical between the 46 studied water bodies. Free-swimming aquatic invertebrates were trapped with the activity trap described in Elmberg et al. (1992). Emerging insects were captured with emergence traps similar to those described by Danell and Sjöberg (1977). Three traps of both types were set per water bodies in different vegetation types for 48 hours. All the water bodies of each area were trapped during one week. The two invertebrate measures were combined to give a water body-level food abundance index (Holopainen et al.,2014) as an index of habitat quality (for more information about local invertebrate catch and species-specific duck-invertebrate associations, see Nummi et al., 2013; Nummi & Väänänen, 2001).

2.4 Statistical methods

Daily survival analysis

The daily survival of forest versus shoreline nests was compared for predation risk, based on 175 nests (88 forest and 87 shoreline nests surrounding in total of 46 water bodies) that survived the entire study period

or with the known depredation time (68 nests depredated). Depredated nests where memory cards of the cameras failed were excluded because of unknown predation date ($N = 2$ in 2017). Furthermore, the daily survival of shoreline nests around permanent lakes and ponds was compared, based on 87 nests (41 with exact depredation time).

The GLMM framework was used to calculate daily nest survival probability by using modified logistic regression, which incorporates the number of exposure days (seven, each beginning at 12 pm) into the link function (Shaffer, 2004). The logistic exposure method is a modification of logistic regression and maximizes the use of nest survival data by treating each measurement day as a discrete trial. Daily nest fate was analysed as a binary response variable (1 = survived, 0 = depredated). In the forest-shoreline comparison explanatory variables were "DATE" (1,...7) and "HABITAT" (factorial: shoreline, forest). As nests were established in pairs around the water bodies, one in the shoreline and one further away from the shoreline, water body ("WETLAND_ID") was used as a random factor. For larger lakes with more than one nest pair, an individual ID was given for every pair of nests. When comparing water body types, the explanatory variables were "DATE" and "TYPE" (factorial: lake, pond). "WETLAND_ID" was used again as a random factor, but this time it only meant shoreline nests. Field percentage ("FIELD") around water bodies was used as an explanatory variable in both analyses. Year effect was found to be negligible during the data exploration and was thus discarded from the analysis.

Pair and brood numbers

Mann-Whitney U-test for independent samples was used to compare the overall pair and brood densities of all the studied duck species between Maaninka and Evo. Furthermore, as mallard and teal are generalist species and common at both study areas, hence providing sufficient data, their pair and brood densities and brood production between the two areas were compared separately. G-test for goodness-of-fit was used to compare species-specific proportions of brooded and non-brooded pairs in 2017 and 2018 at Evo with those at Maaninka.

Pair and brood data were zero-inflated, and when exploring the non-zero part, there was still overdispersion. Thus zero-inflated negative binomial models were used to explain variation in the number of pairs and broods using glmmTMB (Brooks et al., 2017). All the analyses were done in R 3.4.0 (R Core Team, 2017) and the data exploration was done by following the protocol by Zuur et al. (2010). Water body size was controlled for by including shoreline length ("SHORE") as an explanatory variable in all the models. Field percent ("FIELD") was used to indicate the type of the surrounding landscape around each wetland (1 km buffer around the wetland) in every model. The amount of food ("FOOD", continuous) and wetland type ("TYPE", two levels: lake or pond) were used as wetland-level explanatory variables. In addition, pair number ("PAIRS") was included in the models explaining brood numbers. However, as data exploration revealed that pair number and shoreline length were strongly correlated (Pearson correlation r > 0.6), shoreline length was discarded and the pair number was kept, because the latter should more directly determine possible brood production. Due to the nested structure of the data, wetland ID was entered as random factor. Year effect was excluded because it failed to improve model fit. All possible model combinations were fitted. We chose between the best fitting models by using model specific AIC-values and weights (ΔAIC<2, where Δ = AICi – AICmin) (Burnham & Anderson, 2002). Due to model selection uncertainty, we calculated the model-averaged slopes (β-values) of the variables weighted by the Akaike weights and their unconditional standard errors and 95% unconditional confidence intervals; all models in the candidate set were used (see Burnham & Anderson, 2002).

Invertebrate food abundance

Linear mixed-effects modelling (nlme package, Pinheiro et al, 2018) was used to study whether wetland type ("TYPE", two levels: lake or pond) affects the invertebrate food abundance index, incorporating shoreline ("SHORE") and field percentage ("FIELD") as explanatory variables.

RESULTS

3.1 Nest survival

Of the artificial nests, 44% (N =39) were depredated in 2017 and 39% (N = 35) in 2018. The two year average nest predation rate at Evo was 24% and at Maaninka 61%. Wildlife cameras revealed that most common nest predator species were Eurasian magpie (*Pica pica,* 33% of the depredated nests), raccoon dog (*Nyctereutes procyonoides* , 16%), hooded crow (*Corvus corone cornix* , 16%; Figure 2) and Eurasian jay (*Garrulus glandarius* , 11%). To a lesser extent, nests were destroyed by pine martens (*Martes martes,* 7%) and common ravens (*Corvus corax,* 7%), while one nest per species were predated by the American mink (*Neovison vison*), western marsh harrier (*Circus aeruginosus*), common crane (*Crus crus*), European badger (*Meles meles*) and domestic dog (*Canis lupus familiaris*). Two nest predators remained unknown due to camera failure. An average depredation time for the artificial nests was 2.9 days. Only four nests (2 in 2017 and 2 in 2018) were depredated in less than five hours after establishment (minimum 1.5 hours), suggesting that the predators did not follow researchers to the nests.

Daily nest survival was significantly higher in forest compared to shoreline (Table 1). Nest survival also tended to have slight, but significant negative relationship with field percentage around the water bodies. As expected, shoreline nest daily survival was significantly higher around ponds than around lakes (Table 2). Again, nest survival tended to have slight, but significant negative relationship with field percentage around the water bodies.

3.2 Pair and brood numbers, and invertebrate food abundance

Overall brood, but especially pair densities were higher in Maaninka than in Evo (for pairs, $N = 117,$ $U = 378$, $P < 0.001$; for broods, $N = 117$, $U = 863$, $P < 0.001$; Table 3). The same pattern was also observed if only teal densities were considered (pairs $N = 117,$ $U = 495$, $P < 0.001$; broods, $N = 117$, $U = 986$, $P <$ 0.001, Table 3). Mallard pair, but not brood density differed between the areas (pairs $N = 117,$ $U = 884$, $P < 0.001$; broods, $N = 117$, $U = 1267$, $P = 0.242$, Table 3). However, both mallard and teal *per capita* brood production was significantly higher in Evo than in Maaninka (mallard $G = 20.7$, df = 3, $P < 0.001$; teal $G = 52.2$, df = 3, $P < 0.001$; Table 3).

Three best models explained numbers of pairs within ΔAIC <2 (Table 4). The base model (SHORE + FIELD; these variables were included in all model) had the lowest AIC-value. The null model (intercept only) had the poorest fit. Pair numbers increased with shoreline length and field percentage, and ponds had fewer pairs than lakes. Food index appeared not to contribute (Table 5).

Two well-fitting brood models were within ΔAIC < 2 and both included "FOOD" (Table 4). The null model (intercept only) had again the poorest fit. Brood numbers increased with food abundance (Table 5), but less so with number of pairs. Field percentage had only weakly positive, but significant effect on brood numbers.

Water body type had a significant effect for the invertebrate food index. Ponds had higher index than permanent lakes (Table 6), indicating that ponds are more food rich habitats than lakes. Shoreline length or field percentage around the water body did not explain the invertebrate index.

DISCUSSION

Our results indicate that duck densities were higher in the agricultural landscape. However, ducks appear to face a trade-off, because the agricultural landscape also had a higher nest predation rate than the barren forest landscape as revealed by experimental nests equipped with wildlife cameras. Brood production per pair reflected this trade-off: production was higher in the barren forest landscape than in the agricultural landscape, which suggests the occurrence of a high nest predation rate and/or high brood mortality in the agricultural landscape. The results imply that the predator detection at artificial duck nests with wildlife cameras actually reflects their visitation to natural nests. However, our results only concern the early egg-laying period, while predation later in the nest period, during incubation, likely incurs a higher cost to the female.

4.1 Artificial nest survival

Interestingly, corresponding trade-off between food abundance and nest predation risk was not evident at the habitat-level, because ponds rich in food also have the lowest nest predation rates. The wildlife camera data show that the nests on the shores of seasonal, beaver or man-made ponds had higher survival than nests on the shoreline of permanent lakes. Because we tried to keep the nest cover constant between the experimental nests, this difference in survival rates probably arises from more heterogeneous shoreline habitats of ponds and/or the availability of other abundant food resources ponds offer for predators. It has been suggested that nest survival is a combination of large-scale environmental factors and local nest-site characteristics. Landscape productivity can affect general predator and prey abundance, but at the nest-site level vegetation and nest location might affect nest detectability and predator behaviour (Ringelman et al., 2018). For example, predator foraging in the landscape may be concentrated at habitat edges (Andrén, 1995), such as the interface between terrestrial and aquatic habitats. The occurrence of the edge effect may depend on the predator community and predator behaviour (Pasitschniak-Arts et al., 1998), and for instance whether productive wetlands attract and support high number of predators (Stephens et al., 2005).

In the Evo area, mammalian predators have been found to occur more often around beaver ponds than permanent lakes (Nummi et al., 2019b). Still, higher predator occurrence around the beaver ponds was not reflected in the nest predation results, indicating that indeed some habitat-related factors there are working in favour of higher nest survival. It is possible that variability in the shoreline creates circumstances under which predators probably are not able to form long-term search images, i.e. circumstances resembling those considered by Nams (1997) for prey aggregated in space or time. We suggest that because predators may use spatial memory to improve searching efficiency (Phillips et al., 2004), their search around permanent lakes is more regular and effective than around temporally unpredictable ponds. This underlines the potential importance of seasonally flooded ponds for breeding ducks, especially in agricultural areas.

Overall, nest predation risk was lower in forest compared to shoreline nests, indicating occurrence of the edge effect between terrestrial and aquatic ecotones. The pattern was not depending on the fields in the landscape but emerged in both forested and agricultural landscapes. Several currently threatened duck species in Finland are typically nesting near the shoreline (e.g. common pochard *Aythya ferina* , tufted duck), and may suffer from stronger nest predation rates than more flexible nesters (e.g. mallard and teal; e.g. Poysa et al., 2019). Nesting in forest may be safer, but on the other hand, newly hatched ducklings will have to move a long way into water (Poysa & Paasivaara, 2006).

Increased predator abundance and diversity are typical especially for fragmented landscapes (Andren 1995; Pasitschniak-Arts & Messier, 1995). The pattern is particularly pronounced in agricultural landscapes, where there are already high numbers of predators, such as corvids (Andren 1992; Roos 2002; Holopainen et al., 2020a). The results support these observations: nest predation risk was higher in the agricultural landscape, where high rates of corvid predation and richer predator communities were observed with similarly executed wildlife camera-artificial nest experiments (Holopainen et al. 2020a, 2020b). Wildlife camera studies conducted both with artificial nests (Holopainen et al. 2020b) and natural nests (Bell & Conover, 2023) have proven that after the initial depredation event, disturbed nests are often visited by multiple secondary predators. Multiple mammalian visits lead not only to an increased egg depredation rate, but also higher mortality risk for the incubating female. Indeed, hens often abandon (partially) depredated nests and even if incubation is continued, hatching success rate is low (Ackerman et al., 2003; Bell & Conover, 2023).

In Europe, the overall predator populations have increased during last decades threatening bird populations (Roos et al., 2018). In addition to native species, invasive alien predators such as raccoon dog have dispersed widely (Bonesi & Palazon, 2007; Kauhala & Kowalczyk, 2011). Raccoon dog nest predation can be destructive on islands (Dahl & Ahlen, 2018), but its role as mainland duck nest predator has remained unclear (Kauhala, 2004; Kauhala & Auniola, 2001; Nummi et al., 2019a; Sidorovich et al., 2008). Our nest predation results were based on detailed predation information derived from camera trapping. Corvids and raccoon dog were responsible for most of the nest depredation occurred at experimental nests mimicking the situation in the early stage of egg laying (Holopainen at al., 2020a). Without cameras, predator identification is uncertain as it relies on the remains of eggshells or other cues on the nest site (Lariviere, 1999).

8

We recognise that artificial nests give an uncertain reflection of actual nest predation, and thus the intention in this study was not to evaluate actual predation rates but only to study the habitat-specific relative predation risk. Many important differences exist between real and artificial nests that decrease the correspondence and are thus recommended to consider whenever conducting artificial nest experiments (Butler & Rotella, 1998; Whelan et al., 1994; Wilson & Brittingham, 1998; Part & Wretenberg, 2002). Effort was put in to tackle the uncertainties: real mallard eggs were used and the species observed in the camera pictures are known predators of real duck nests (Opermanis et al., 2001; Poysa et al., 1997), and therefore it is assumed that the observed species do not differ from the actual nest predator assemblage. As Anthony et al. (2006) showed with dusky Canada geese (*Branta canadensis occidentalis*) artificial nests can be used to identify the potential nest predator species and that the predator species ratios can correspond those of the real nests. Our artificial nest density was low ensuring that observations were independent. The lacking hen problem was avoided by focusing only on the early egg-laying stage when females are not on their nests, so the set-up resembles the actual situation.

Compared to natural nests, the use of cameras may affect nest survival, typically by decreasing the predation rate (Richardson, et al, 2009); this is a potential shortcoming that could not be avoided. It is also acknowledged that this study design potentially emphasises the role of visual predators, such as corvids, as nests were not necessarily hidden as efficiently as a dabbling duck hen's nest would be. High corvid predation rates may also be expected to occur at the early real nests, as the duck nest predation rate in North America during the early part of the breeding season was observed to positively relate to American crow (*Corvus brachyrhynchos*) activity (Johnson et al., 1989).

The correspondence of the artificial nests with actual nest success cannot be assessed, but brood production rates in the study areas have been measured, which can be used as a rough estimate of predation pressure. While there are still uncertainties in this method, we emphasise that the problems underlined by the earlier studies have been considered and the differences between real and artificial nests were accordingly minimized; thus, we suggest that our data are suitable for detecting trends in predation rates in relation to habitat (Wilson & Brittingham, 1998).

Invertebrate food abundance

As expected, ponds (seasonal, beaver and man-made) were more invertebrate-rich habitats than permanent lakes, while contrary to the hypothesis, the percentage of field land around the wetlands did not influence invertebrate index. Selecting a pond instead of a lake as a breeding habitat would thus simultaneously minimize nest predation risk and maximize food availability in any landscape.

Habitat use of duck pairs was not associated with invertebrate food, whereas duck broods preferred habitats richer in food. The number of broods at the water bodies was only weakly dependent on the number of pairs, which can be a reflection of differing habitat requirements of pairs and broods (Holopainen et al., 2015) or high nest predation and brood mortality. Sjoberg et al. (2000) showed for mallards that all lakes used by pairs are not suitable for broods, the difference in lake use between pairs and broods being due to food limitation at the brood stage (Gunnarsson et al. , 2004). In boreal lakes food limitation can be intensified due to food competition between ducks and fish (Nummi et al., 2016). Income breeders, like teal, seem to avoid brood-stage food limitation by congregating in beaver ponds and seasonal ponds where invertebrate production is high and the habitat structure favourable for brood foraging (Nummi & Hahtola, 2008; Nummi & Holopainen 2014). In Evo it is known that teal brood production is following the flood dynamics created by the beaver and spring floods (Holopainen et al., 2014).

Interestingly, the results did not show that duck pairs or broods used ponds more than permanent lakes. This contradicts the earlier long-term results from the Evo area (Nummi & Holopainen, 2014). It is possible that ducks visit food-rich ponds for foraging in very short periods, reducing the ability to detect them there (Nummi et al., 2019c). Waterbird species may also differ in their ability to respond to environmental factors, such as habitat variability (Wiens, 1976; Nummi & Poysa, 1997). For example, lapwings (*Vanellus vanellus*) are known to nest in higher densities around flooded footdrains, and chicks forage on the wet mud around

these wet features supporting invertebrate rich habitats (Eglington et al., 2008, 2010).

Conservation implications

Successful management of ducks would demand understanding of the relationship between habitat availability and predators (Drever et al., 2004). This study emphasizes the benefits of the availability of different water body types for breeding ducks. It showed that flooded and/or seasonal ponds might be especially good habitats. It seems that two important limiting factors of the breeding season – nest survival and amount of invertebrate food – are higher there than on permanent lakes.

Kubelka et al. (2018) showed that shorebirds have experienced a worldwide increase in nest predation over the past decades and that the pattern is especially pronounced in the high northern latitudes. 12 of the 19 duck species living in Finland are already classified as threatened to some degree by the Finnish red list (Lehikoinen et al., 2019), underlining the urgent need for conservation actions. These results indicate that while duck pair and brood densities are higher in an agricultural landscape, brood production seems to be higher in forested landscapes with lower nest predation rates. Thus, duck species nesting at eutrophic lakes in agricultural areas and preferring especially shorelines as nesting places, may suffer from high nest predation rates, which may contribute to the declining population trends (Lehikoinen et al., 2016; Poysa & Linkola, 2021). It is suggested that the nest predation pressure around these lakes has increased due to the appearance of alien predators (Holopainen et al., 2021; Poysa & Linkola, 2021) and the disappearance of protective umbrella species; for instance, loss of black-headed gull *Chroicocephalus ridibundus* colonies removes a local protective "umbrella" of mobbing gulls, in a way that is thought to expose the nests of associated waterbird to greater predation threat (Poysa et al., 2019). Controlling predators, especially alien species, would thus be an important conservation action to improve duck breeding success (Dahl & Ahlen, 2018; Garrettson & Rohwer, 2001; Jaatinen et al., 2022).

Seasonal pond ecosystems in the boreal biome remain poorly studied, even so that in Finland the habitat type does not have a conservation status evaluation done due to lacking information (Lammi et al. 2018). Nevertheless, seasonal pond habitats are commonly not protected. The loss of seasonal ponds has been dramatic in boreal biome due to drainage, destruction and water regulation (Colburn, 2004), also in Finland (Kuusisto et al., 1998). Furthermore, it is predicted that climate change will reduce the extent of snowmelt dependant spring flooding in the future (Veijalainen et al., 2010). In addition to wetland restoration and blocking up drains, the lack of flooded waters may be mitigated by favouring beavers (Hood & Bayley, 2008; Nummi & Holopainen, 2020) or man-made wetlands (Danell & Sjoberg, 1982; Eglington et al., 2008; Čehovská et al., 2022).

REFERENCES

Ackerman, J.T., Eadie, J.M., Yarris, G.S., Loughman, D.L., & McLandress, M.R. (2003). Cues for investment: nest desertion in response to partial clutch depredation in dabbling ducks. *Animal Behaviour,* 66: 871–883 DOI: 10.1006/anbe.2003.2283.

Andrén, H. (1992). Corvid density and nest predation in relation to forest fragmentation: A landscape perspective. *Ecology* , 73, 794–804. DOI: 10.2307/1940158.

Andrén, H. (1995). Effects of landscape composition on predation rates at habitat edges. In L. Hansson, L. Fahrig, and G. Merriam (Eds.)*Mosaic landscapes and ecological processes* (pp. 225–255). Dordrecht: Springer, Chapman and Hall.

Anthony, R.M., Grand, J.B., Fondell, T.F., & Miller, D.A. (2006). Techniques for identifying predators of goose nests. *Wildlife biology,* 12, 249–256. DOI: 10.2981/0909-6396(2006)12[249:TFIPOG]2.0.CO;2

Bonesi, L., & Palazon, S. (2007). The American mink in Europe: Status, impacts, and control. *Biological Conservation,* 134, 470–483. DOI:10.1016/j.biocon.2006.09.006

Brides, K., Wood, K. ., Hearn, R.D., & Fijen, T.P. M. (2017). Changes in the sex ratio of the Common Pochard *Aythya ferina* in Europe and North Africa. *Wildfowl* , 67, 100–112.

Brooks, M. E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C. W., Nielsen, . . . Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* , 9, 378–400. DOI: 10.3929/ethz-b-000240890

Burnham, K.P., & Anderson, D.R. (2002). Model selection and multimodel inference. A practical information-theoretic approach (2nd ed.). New York: Springer.

Butler, M.A., & Rotella, J. J. (1998). Validity of using artificial nests to assess duck-nest success. *The Journal of Wildlife Management* , 62, 163–171. DOI: 10.2307/3802274

Čehovská, M., Kattainen, S., Väänänen, V.-M., Putaala, A., & Nummi, P. (2022). Compensating freshwater habitat loss—duck productivity and food resources in man-made wetlands. *European Journal of Wildlife Research* , *68* , 35. DOI: 10.1007/s10344-022-01577-8.

Colburn, E.A. (2004). Vernal Pools. Natural history and conservation. Blacksburg, Virginia: The McDonald and Woodward Publishing Company.

Bell, M.E., & Conover, M.R. (2023). Predator and duck behaviours at depredated nests in wetlands of Great Salt Lake, Utah. *Behaviour* 160: 463–487. DOI: 10.1163/1568539X-bja10217

Dahl, F., & Åhlén, P.A. (2018). Nest predation by raccoon dog *Nyctereutes procyonoides* in the archipelago of northern Sweden. *Biological Invasions* , 1–13. DOI: 10.1007/s10530-018-1855-4.

Danell, K., & Sjöberg, K. (1977). Seasonal emergence of chironomids in relation to egglaying and hatching of ducks in a restored lake (northern Sweden). *Wildfowl* , 28, 129–135.

Danell, K., & Sjöberg, K. (1982). Successional patterns of plants, invertebrates and ducks in a man-made lake. *Journal of Applied Ecology* . 14, 395–409. DOI: 10.2307/2403475

Davidson, N.C. (2014). How much wetland has the world lost? Long-term and recent trends in global wetland area. *Marine and Freshwater Research* , 65, 934–941. DOI: 10.1071/MF14173

Drever, M.C. Wins-Purdy, A., Nudds, T.D. & Clark, R.G. (2004). Decline of duck nest success revisited: relationships with predators and wetlands in dynamic prairie environments. *The Auk,* 121:497-508.

Eglington, S. M., Gill, J. A., Bolton, M., Smart, M. A., Sutherland, W. J., & Watkinson, A. R. (2008). Restoration of wet features for breeding waders on lowland grassland. *Journal of Applied Ecology* , 45, 305–314. DOI: 10.1111/j.1365-2664.2007.01405.x

Eglington, S.M., Bolton, M., Smart, M.A., Sutherland, W.J., & Watkinson, A.R. (2010). Managing water levels on wet grasslands to improve foraging conditions for breeding northern lapwing *Vanellus vanellus* . *Journal of Applied Ecology* , 47, 451–458. DOI: 10.1111/j.1365-2664.2010.01783.x

Elmberg, J., Nummi, P., Pöysä, H., & Sjöberg, K. (1992). Do intruding predators and trap position affect the reliability of catches in activity traps? *Hydrobiologia* , 239, 187–193. DOI: 10.1007/BF00007676

Fox, A.D., Jørgensen, H. E., Jeppesen, E., Lauridsen, T.L., Søndergaard, M., Fugl, K., Myssen, P., Balsby, T.J.S. & Clausen, P. (2020). Relationships between breeding waterbird abundance, diversity, and clear water status after the restoration of two shallow nutrient-rich Danish lakes. *Aquatic Conservation: Marine and Freshwater Ecosystems* . 30, 237–245. DOI:10.1002/aqc.3260

Garrettson, P.R., & Rohwer, F.C. (2001). Effects of mammalian predator removal on production of upland-nesting ducks in North Dakota. *The Journal of Wildlife Management* , 65, 398–405. DOI: 10.2307/3803091

Gibbs, J.P. (2000). Wetland loss and biodiversity conservation.*Conservation Biology* , 14, 314–317. DOI: 10.1046/j.1523-1739.2000.98608.x

Guillemain, M., Pöysä, H., Fox, A.D., Arzel, C., Dessborn, L., Ekroos, J., Gunnarsson, G., Holm, T.E., Christensen, T.K., Lehikoinen, A., Mitchell, C., Rintala, J.A., & Møller, A.P. (2013). Effects of climate change on European ducks: What do we know and what do we need to know?*Wildlife Biology* , 19, 404–419. DOI: 10.2981/12-118

Gunnarsson, G., & Elmberg, J. (2008). Density-dependent nest predation – an experiment with simulated Mallard nests in contrasting landscapes.*Ibis* . 150, 259–269. DOI:10.1111/j.1474-919X.2007.00772.x

Gunnarsson, G., Elmberg, J., Sjöberg, K., Pöysä, H., & Nummi, P. (2004). Why are there so many empty lakes? Food limits survival of mallard ducklings. *Canadian Journal of Zoology* , 82, 1698–1703. http://dx.doi.org/10.1139/Z04-153

Halley, D.J., Saveljev, A.P. & Rosell, F. (2021). Population and distribution of beavers *Castor fiber* and *Castor canadensis*in Eurasia. Mammalian Review, 51: 1-24. DOI: 10.1111/mam.12216.

Holopainen, S., Arzel, C., Dessborn, L., Elmberg, J., Gunnarsson, G., Nummi, P., Pöysä, H., & Sjöberg, K. (2015). Habitat use in ducks breeding in boreal freshwater wetlands: A review. *European Journal of Wildlife Research* , 61, 339–363. DOI: 10.1007/s10344-015-0921-9

Holopainen, S. & Lehikoinen, A. (2021). Role of forest ditching and agriculture on water quality: Connecting the long-term physico-chemical subsurface state of lakes with landscape and habitat structure information. *Science of The Total Environment,* 806, 4, 151477. DOI: 10.1016/j.scitotenv.2021.151477

Holopainen, S., Nummi, P., & Pöysä, H. (2014). Breeding in the stable boreal landscape: Lake habitat variability drives brood production in the teal (*Anas crecca*). *Freshwater Biology* , 59, 2621–2631. DOI: 10.1111/fwb.12458

Holopainen, S., Väänänen, V.-M., & Fox, A.D. (2020a) Landscape and habitat affect frequency of artificial duck nest predation by native species, but not by an alien predator. *Basic and Applied Ecology,*48, 52–60. DOI: 10.1016/j.baae.2020.07.004

Holopainen, S., Väänänen, V.-M., & Fox, A.D. (2020b). Artificial nest experiment reveals inter-guild facilitation in duck nest predation.*Global Ecology and Conservation,* e01305. DOI: 10.1016/j.gecco.2020.e01305

Holopainen, S., Väänänen, V-M., Vehkaoja, M., & Fox, A.D. (2021). Do alien predators pose a particular risk to duck nests in Northern Europe? Results from an artificial nest experiment. *Biological Invasions,*23, 3795–3807. DOI: 10.1007/s10530-021-02608-2.

Hood, G. A., & Bayley, S. E. (2008). Beaver (*Castor canadensis*) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada. *Biological Conservation* , 141, 556–567. DOI: 10.1016/j.biocon.2007.12.003

Hu, S., Niu, Z., Chen, Y., Li, L., & Zhang, H. (2017). Global wetlands: Potential distribution, wetland loss, and status. *Science of the Total Environment* , 586, 319–327.

Jaatinen, K., Hermansson, I., Mohring, B., Steele, B.B., & Öst, M. (2022). Mitigating impacts of invasive alien predators on an endangered sea duck amidst high native predation pressure. *Oecologia* , 198, 543–552. DOI: 10.1007/s00442-021-05101-8.

Johnson, D.H., Sargeant, A.B., & Greenwood, R.J. (1989). Importance of individual species of predators on nesting success of ducks in the Canadian Prairie Pothole Region. *Canadian Journal of Zoology,* 67, 291–297. DOI: 10.1139/z89-043

Kauhala, K. (2004). Removal of medium-sized predators and the breeding success of ducks in Finland. *Folia Zoologica* . 53, 367–378.

Kauhala, K., & Auniola, M. (2001). Diet of raccoon dogs in summer in the Finnish archipelago. *Ecography* , 24, 151–156. DOI: 10.1034/j.1600-0587.2001.240205.x

Kauhala, K., & Kowalczyk, R. (2011). Invasion of the raccoon dog *Nyctereutes procyonoides* in Europe: History of colonization, features behind its success, and threats to native fauna. *Current Zoology* , 57, 584–598. DOI: 10.1093/czoolo/57.5.584

Kauppinen, J., & Väisänen, R. (1993). Ordination and lake classification of waterfowl communities in south boreal lakes. Finnish Game Research 48, 3–23.

Kingsford, R.T., Basset. A., & Jackson, L. (2016). Wetlands: Conservation's poor cousins. *Aquatic Conservation: Marine and Freshwater Ecosystems* , 26: 892–916. DOI: 10.1002/aqc.2709

Koskimies, P., & Väisänen, R. A. (Eds.) (1991). Monitoring bird populations: A manual of methods applied in Finland. Helsinki: Zoological Museum, Finnish Museum of Natural History, University of Helsinki.

Kubelka, V., Šálek, M., Tomkovich, P., Végvári, Z., Freckleton, R. P., & Székely, T. (2018). Global pattern of nest predation is disrupted by climate change in shorebirds. *Science* , 362, 680-683. DOI: 10.1126/science.aat8695.

Kuusisto, E., Bäck, S., Vuoristo, H., Mannio, J., & Lappalainen, I. (1998). Vesiluonto osana ihmisen taloutta (In Finnish: Aquatic nature as part of human economy). In: I. Lappalainen (Ed.), *Suomen luonnon monimuotoisuus* . Helsinki: Oy Edita Ab.

Larivière, S. (1999). Reasons why predators cannot be inferred from nest remains. *The Condor* , 101, 718–721. DOI: 10.2307/1370209

Lammi et al. (2018). Sisävedet ja rannat (Inland waters and shores). In Kontula & Raunio (eds) Suomen luontotyyppien uhanalaisuus 2018 Luontotyyppien punainen kirja. Osa 1 – tulokset ja arvioinnin perusteet (Threatened habitat types in Finland 2018. Red List of habitats. Part I: Results and basis for assessment) (In Finnish)

Larmola, T., Alm, J., Juutinen, S., Saarnio, S., Martikainen, P. J., & Silvola, J. (2004). Floods can cause large interannual differences in littoral net ecosystem productivity. *Limnology and Oceanography* , 49, 1896–1906. DOI: 10.4319/lo.2004.49.5.1896

Lehikoinen, A., Jukarainen, A., Mikkola-Roos, M., Below, A., Lehtiniemi, T., Pessa, J., . . . Liukko, U.-M. (Eds.) (2019). Suomen lajien uhanalaisuus - Punainen kirja 2019 (In Finnish with English summary: The 2019 Red List of Finnish Species). Helsinki: Ympäristöministeriö, Suomen ympäristökeskus.

Lehikoinen, A., Rintala, J., Lammi, E., & Pöysä, H. (2016). Habitat-specific population trajectories in boreal waterbirds: Alarming trends and bioindicators for wetlands. *Animal Conservation* , 19, 88–95. DOI: 10.1111/acv.12226

Leivo, M., Asanti, T., Koskimies, P., Lammi, E., Lampolahti, J., Mikkola-Roos, M., & Virolainen, E. (2002). Suomen tärkeät lintualueet FINIBA (In Finnish: Imprtant bird areas of Finland FINIBA). BirdLife Suomen julkaisuja nro 4. Kuopio: Suomen graafiset palvelut.

Lindén, H., Hario, M., & Wikman, M. (1996). Riistan jäljille. (In Finnish with English summary: Follow the game). Helsinki: Riista- ja kalatalouden tutkimuslaitos, Edita.

Ma, Z., Cai, Y., Li, B., & Jiakuan, C. (2010). Managing wetland habitats for waterbirds: An international perspective. *Wetlands* , 30, 15–27. DOI: 10.1007/s13157-009-0001-6

McMenamin, S.K., Hadly, E.A., & Wright, C.K. (2008). Climatic change and wetland desiccation cause amphibian decline in Yellowstone National Park. *PNAS.* 105, 16988–16993. DOI: 10.1073/pnas.0809090105

Nams, V.O. (1997). Density-dependent predation by skunks using olfactory search images. *Oecologia* , 110, 440–448. DOI: 10.1007/s004420050179

Nummi, P., & Hahtola, A. (2008). The beaver as an ecosystem engineer facilitates teal breeding. *Ecography* , 31, 519–524. DOI: 10.1111/j.0906-7590.2008.05477.x

Nummi, P., & Holopainen, S. (2014). Whole-community facilitation by beaver: Ecosystem engineer increases waterbird diversity. *Aquatic Conservation: Marine and Freshwater Ecosystems* . 24, 623–633. DOI: 10.1002/aqc.2437

Nummi, P., & Holopainen, S. (2020). Restoring wetland biodiversity using research: Whole-community facilitation by beaver as framework. *Aquatic Conservation: Marine and Freshwater Ecosystems* , 30, 1798–1802. DOI: 10.1002/aqc.3341

Nummi, P., Liao, W., Huet, O., Scarpulla, E., & Sundell, J. (2019b). The beaver facilitates species richness and abundance of terrestrial and semi-aquatic mammals. *Global Ecology and Conservation* , 20, e00701. DOI: 10.1016/j.gecco.2019.e00701

Nummi, P., Paasivaara, A., Suhonen, S. & Poysa, H. (2013). Wetland use by brood-rearing female ducks in a boreal forest landscape: The importance of food and habitat. *Ibis* 155, 68-79.

Nummi P., & Poysa H. (1997). Population and community level responses in Anas-species to patch disturbance caused by an ecosystem engineer, the beaver. *Ecography* , 20, 580–584. DOI: 10.1111/j.1600-0587.1997.tb00426.x

Nummi, P., Suontakanen, E.-M., Holopainen S., & Vaananen, V.-M. (2019c). The effect of beaver facilitation on Common Teal: Pairs and broods respond differently at the patch and landscape scales.*Ibis* , 161, 301–309. DOI: 10.1111/ibi.12626

Nummi, P., & Vaananen, V-M. (2001). High overlap in diets of sympatric dabbling ducks – an effect of food abundance? *Annales Zooligici Fennici* 38, 123–130.

Nummi, P., Vaananen, V.-M., Holopainen S., & Poysa H. (2016). Duck–fish competition in boreal lakes – a review. *Ornis Fennica* , 93, 67–76.

Nummi, P., Vaananen, V-M., Pekkarinen, A-J., Eronen, V., Mikkola-Roos, M., Nurmi, J., Rautiainen, A., & Rusanen, P. (2019a). Alien predation in wetlands – Raccoon Dog and waterbird breeding success. *Baltic Forestry,* 25, 228–237.

Opermanis, O., Mednis, A., & Bauga, I. (2001). Duck nests and predators: Interaction, specialisation and possible management.*Wildlife Biology* , 7, 87–96.

Part, T., & Wretenberg, J. (2002). Do artificial nests reveal relative nest predation risk for real nests? *Journal of Avian Biology* , 33, 39–46. DOI: 10.1034/j.1600-048X.2002.330107.x

Pasitschniak-Arts, M., Clark, R. G. & Messier, F. (1998). Duck nesting success in a fragmented prairie landscape: Is edge effect important?*Biological Conservation* , 85, 55–62. DOI: 10.1016/S0006-3207(97)00143-2

Pasitschniak-Arts, M., & Messier, F. (1995). Risk of predation on waterfowl nests in the Canadian prairies: Effects of habitat edges and agricultural practices. *Oikos* , 73, 347–355. DOI: 10.2307/3545958

Phillips, M. L., Clark, W.R., Nusser, S. M., Sovada, M.A. & Greenwood, R.J. (2004). Analysis of predator movement in prairie landscapes with contrasting grassland composition. *Journal of Mammalogy* , 85, 187–195. DOI: 10.1644/15451542(2004)085<0187:AOPMIP>2.0.CO;2

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team (2018). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-137, https://CRAN.R-project.org/package=nlme.

Pirkola, M.K., & Hogmander J. (1974). Sorsapoikueiden ianmaaritys (In Finnish, English summary: The age determination of duck broods in the field). *Suomen Riista* , 25, 50–55.

Poysa, H. (1996). Population estimates and the timing of waterfowl censuses. *Ornis Fennica* , 73, 60–68.

Poysa, H. (2019). Tracking ice phenology by migratory waterbirds: settling phenology and breeding success of species with divergent population trends. *Journal of Avian Biology* , e02327. DOI: 10.111/jav.02327

Poysa, H., Lammi, E., Poysa, S., & Vaananen, V.-M. (2019). Collapse of a protector species drives secondary endangerment in waterbird communities. *Biological Conservation* , 230, 75–81. DOI: 10.1016/j.biocon.2018.12.016

Poysa, H., & Linkola, P. (2021). Extending temporal baseline increases understanding of biodiversity change in European boreal waterbird communities. *Biological Conservation,* 257, 109139. https://doi.org/10.1016/j.biocon.2021.109139

Poysa, H., Milonoff, M., & Virtanen, J. (1997). Nest predation in hole-nesting birds in relation to habitat edge: An experiment. *Ecography* , 20, 329-335. DOI: 10.1111/j.1600-0587.1997.tb00377.x

Poysa, H., & Paasivaara, A. (2006). Movements and mortality of common goldeneye *Bucephala clangula* broods in a patchy environment. *Oikos* , 115, 33–42. DOI: 10.1111/j.2006.0030-1299.15036.x

Poysa, H., Rintala, J., Lehikoinen, A., & Vaisanen, R.A. (2013). The importance of hunting pressure, habitat preference and life history for population trends of breeding waterbirds in Finland. *European Journal of Wildlife Research* , 59, 245–256. DOI: 10.1007/s10344-012-0673-8

QGIS Development Team (2017). QGIS Geographic Information System. Open Source Geospatial Foundation Project. URL http://qgis.osgeo.org.

R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Ramsar Convention Secretariat (2010). Wise use of wetlands: Concepts and approaches for the wise use of wetlands. Ramsar handbooks for the wise use of wetlands (4th ed.), vol. 1. Gland: Ramsar Convention Secretariat.

Richardson, T.W., Gardali, T., & Jenkins, S.H. (2009). Review and meta-analysis of camera effects on avian nest success. The Journal of *Wildlife Management* , 73, 287–293. DOI: 10.2193/2007-566

Ringelman, K.M., Walker, J., Ringelman, J.K., & Stephens S.E. (2018). Temporal and multi-spatial environmental drivers of duck nest survival. *The Auk* , 135, 486-494. DOI: 10.1642/AUK-17-207.1.

Roos, S. (2002). Functional response, seasonal decline and landscape differences in nest predation risk. *Oecologia* , 133, 608–615. DOI: 10.1007/s00442-002-1056-8.

Roos, S., Smart, J., Gibbons, D.W., & Wilson, J.D. (2018). A review of predation as a limiting factor for bird populations in mesopredator-rich landscapes: A case study of the UK. *Biological reviews* , 93, 1915–1937. DOI: 10.1111/brv.12426.

Shaffer, T.L. (2004). A unified approach to analyzing nest success. *The Auk* , 121, 526–540. DOI: 10.1642/0004-8038(2004)121[0526:AUATAN]2.0.CO;2

Sidorovich, V.E., Solovej, I.A., Sidorovich, A.A., & Dyman A.A. (2008). Seasonal and annual variation in the diet of the raccoon dog *Nyctereutes procyonoides* in northern Belarus: The role of habitat type and family group. *Acta Theriologica* , 53, 27–38. DOI: 10.1007/BF03194276

Sievers, M., Hale, R., Parris, K.M., & Swearer, S.E. (2018). Impacts of human-induced environmental change in wetlands on aquatic animals. *Biological Reviews* , 93, 529–554. DOI: 10.1111/brv.12358

Sjoberg, K., Poysa, H., Elmberg, J., & Nummi, P. (2000). Response of Mallard ducklings to variation in habitat quality: An experiment of food limitation. *Ecology* , 81, 329–335. DOI: 10.1890/0012-9658(2000)081[0329:ROMDTV]2.0.CO;2

Stephens, S.E., Rotella, J.J., Lindberg, M.S., Taper, M.L., & Ringelman, J.K. (2005). Duck nest survival in the Missouri Coteau of North Dakota: Landscape effects at multiple spatial scales.*Ecological Applications* , 15, 2137–2149. DOI: 10.1890/04-1162

Uusihakala, L. (2021). Metson haasteet Nuuksiossa –maiseman vaikutus pesapredaatioon ja supikoiraan pesasaalistajana (The challenges of the capercaillie in the Nuuksio national park – the effect of landscape on the nest predation and the raccoon dog). Master Thesis, University of Helsinki, Faculty of Biologicl and Environmental Sciences. In Finnish. Available at https://ethesis.helsinki.fi/repository/handle/123456789/35316

Vaananen, V.-M., Poysa, H., & Runko, P. (2016). Nest and brood stage association between duck and small colonial gulls in boreal wetlands.*Ornis Fennica* , 93, 47–54.

Valkama, J., Vepsalainen, V., & Lehikoinen, A. (2011). Suomen III Lintuatlas (In Finnish: Third bird atlas of Finland). Luonnontieteellinen keskusmuseo, ymparistoministerio. <http://atlas3.lintuatlas.fi> ISBN 978-952-10-6918-5. (In Finnish)

Veijalainen, N., Lotsari, E., Alho, P., Vehvilainen, B., & Kayhko, J. (2010). National scale assessment of climate change impacts on flooding in Finland. *Journal of Hydrology* , 391, 333–350. DOI: 10.1016/j.jhydrol.2010.07.035

Whelan, C. J., Dilger, M. L., Robson, D. Hallyn, N. & Dilger, S. (1994). Effects of olfactory cues on artificial-nest experiments.*Auk* , 111: 945–952.

Wiens, J. A. (1976). Population responses to patchy environments.*Annual Review of Ecology and Systematics* , 7, 81–120.

Wilson, G. R., & Brittingham, M. C. (1998). How well do artificial nests estimate success of real nests? *Condor* , 100, 357–364. DOI: 10.2307/1370277

Zuur A.F., Ieno E.N., & Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1, 3–14. DOI: 10.1111/j.2041-210X.2009.00001.x

TABLE 1 Model estimate for the daily survival rate of artificial nests on shoreline and forest. DATE = exposure day (1...7), HABITAT = Forest (categorical factor, shoreline represented by intercept), FIELD = field percentage within 1 000 m buffer zone around the wetland. Random effect standard deviation for WETLAND_ID = 0.69.

	Estimate	SE	z-value	P
(Intercept)	2.182	0.373	5.856	< 0.001
DATE	0.512	0.077	6.671	< 0.001
HABITAT (Forest)	0.708	0.266	2.661	0.008
FIELD	-0.021	0.006	-3.719	< 0.001

TABLE 2 Model estimate for the daily survival rate of artificial nests on lake and pond shoreline. DATE = exposure day (1...7), HABITAT = Pond (categorical factor, lake represented by intercept), FIELD = field percentage within 1 000 m buffer zone around the wetland. Random effect standard deviation for WETLAND_ID = 1.12.

	Estimate	SE	z-value	P
(Intercept)	1.983	0.603	3.286	0.001
DATE	0.473	0.125	3.783	< 0.001

	Estimate	SE	z-value	P
TYPE (Pond)	1.122	0.534	2.102	0.036
FIELD	-0.029	0.009	-3.089	0.002

TABLE 3 The average and range of pair and brood densities (all duck species, teal, mallard/shoreline km) and brood production of teal and mallard in Evo and Maaninka combining the years 2017–2018.

	Pairs/ shoreline km Average, median (range)	Broods/ shoreline km Average, median (range)	Broods/ pair
All species			
Evo	0.9, 0.0 $(0-9.1)$	0.3, 0.0 $(0-4.5)$	
Maaninka	5.1, 3.8 $(0-23.1)$	1.1, 0.3 $(0-15.2)$	
Teal			
Evo	0.4, 0.0 $(0-9.1)$	0.2, 0.0 $(0-4.5)$	0.35
Maaninka	2.1, 1.4 $(0-10.9)$	0.5, 0.0 $(0-4.5)$	0.13
Mallard			
Evo	0.5, 0.0 $(0-6.8)$	0.1, 0.0 $(0-2.3)$	0.26
Maaninka	1.5, 0.6 $(0-7.1)$	0.2, 0.0 $(0-1.7)$	0.11

TABLE 4 Models explaining the number of pairs and broods. Only best models with ΔAIC<2, where $\Delta =$AIC$_i$ – AIC$_{min,}$ are shown. TYPE = lake or pond, SHORE = wetland shoreline (km), FOOD = invertebrate food index, FIELD = field percentage within 1 000 m buffer zone around the wetland.

| Model	df	AIC	ΔAIC	w
Pairs				
SHORE + FIELD	6	322.886	0.000	0.424
TYPE + SHORE + FIELD	7	323.645	0.759	0.290
FOOD + SHORE + FIELD	7	324.850	1.964	0.159
Intercept only	1	348.806	25.920	0.000
Broods				
FOOD + PAIRS + FIELD	7	178.883	0.000	0.656
FOOD + TYPE + PAIRS + FIELD	8	180.331	1.448	0.318
Intercept only	1	192.818	13.935	0.000

TABLE 5 Model averaged parameter estimates, their standard errors and unconditional 95 % confidence intervals from models explaining habitat use of pairs and broods. Estimates are based on all models in the candidate model set using Akaike weights as weighting factors. CI = confidence interval, TYPE = pond (compared to lake), SHORE = wetland shoreline (km), FOOD = invertebrate food index, FIELD = field percentage within 1 000 m buffer zone around the wetland.

		SE	95% CI	95% CI
	Estimate		Lower	Upper
Pairs				
FOOD	0.013	0.007	-0.001	0.028
TYPE (pond)	-0.490	0.038	-0.579	-0.429
SHORE	0.297	0.022	0.247	0.336
FIELD	0.028	0.000	0.026	0.029

		SE	95% CI	95% CI
Broods				
FOOD	0.144	0.006	0.132	0.158
TYPE (pond)	-0.331	0.365	-0.719	0.874
PAIRS	0.066	0.012	0.058	0.105
FIELD	0.006	0.001	0.005	0.011

,

TABLE 6 Parameters of the model explaining invertebrate food index. TYPE = pond (lake presented by intercept), SHORE = wetland shoreline (km), FIELD = field percentage within 1 000 m buffer zone around the wetland. Random effect standard deviation for WETLAND_ID = 3.373.

	Estimate	SE	t-value	p-value
Intercept	0.671	1.424	0.471	0.640
TYPE (pond)	3.618	1.604	2.256	0.030
SHORE	-0.284	0.512	-0.554	0.582
FIELD	0.036	0.026	1.408	0.166
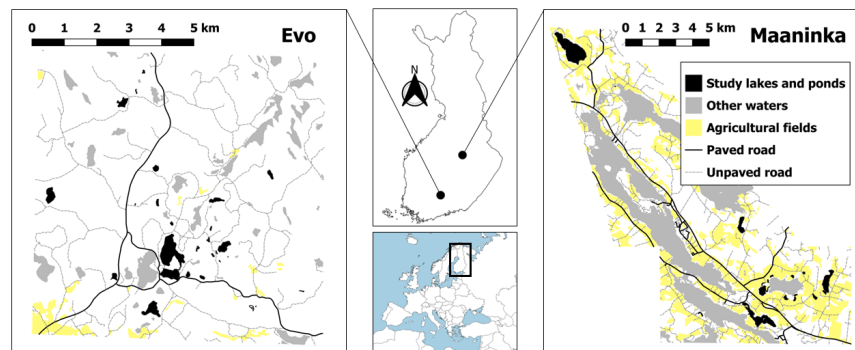
of Finland)

Fig 1. Location of Finland in Europe and the maps of the study areas. (Sources: Esri, National Land Survey)
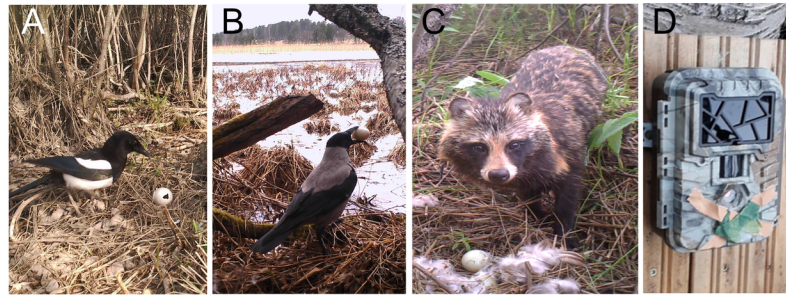
18

Fig. 2. Wildlife cameras revealed that the most common nest predator species were A) Eurasian magpie (photo by Niteforce Professional Trail Camera 12 MP), B) hooded crow (photo by Uovision UV595-Full HD 12MP) and C) raccoon dog (still from video by Uovision with +2 eyeglass lens). D) To adjust the focus of wildlife cameras into less than 1 meter, we attached +2 eyeglass lens ("backwards") in front of the wildlife camera lens. Tape was then camouflaged.

FUNDING INFORMATION
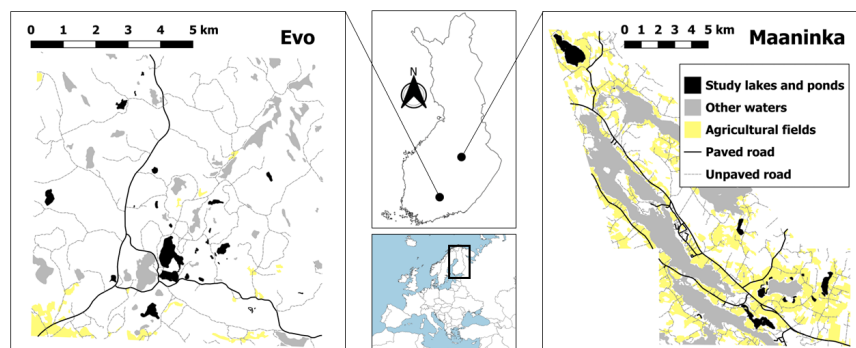
CONFLICT OF INTEREST STATEMENT

We declare that the authors of this article have no conflicts of interest.
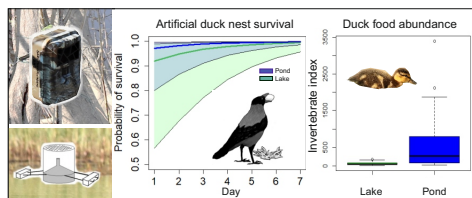
DATA AVAILABILITY STATEMENT

We confirm that the entire database used in this article is available in the Appendix and supplementary material of this manuscript.

AUTHOR CONTRIBUTIONS

Idea for this study was from SH, PN and V-MV. SH, EM, PN and V-MV contributed to the field work. SH did statistical analyses. All authors contributed to the writing process.

Hosted file

Fig 2.eps available at https://authorea.com/users/628413/articles/648996-balancing-between-predation-risk-and-food-by-boreal-breeding-ducks