

Invertebrate biomass and richness and shoreline length are key drivers of duck breeding success in boreal constructed wetlands

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Research Article

Keywords: wetland creation, man-made wetlands, breeding ducks, aquatic invertebrates, agricultural habitat

Posted Date: October 8th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-11014455/v1>

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Additional Declarations: No competing interests reported.

Abstract

Constructed wetlands are increasingly used to offset the loss of duck breeding habitat. To assess their effectiveness, we evaluate how food supply, habitat characteristics, and predation are associated with duck pairs, broods, and ducklings at 44 constructed wetlands for waterbirds in Finland. We also conducted separate species-level analyses for the most common boreal ducks: mallard (*Anas platyrhynchos*), common teal (*Anas crecca*), common goldeneye (*Bucephala clangula*), and Eurasian wigeon (*Mareca penelope*).

Our results show that food resources and their availability are key drivers of breeding ducks. Higher invertebrate biomass and species richness, together with longer shoreline length (including both wetland and island shoreline), were the main features explaining high duck abundances across all breeding stages and at the species level. Agricultural habitat was the most influential habitat variable, showing a positive association with mallard pairs. In contrast, brood abundance was negatively correlated with the proportion of agricultural land surrounding the wetland. Common teal pair and mallard brood abundances were negatively associated with the occurrence of mammalian predators. Contrary to our expectations, the number of islands (expressed by 3 groups) was not an important habitat characteristic for breeding ducks. Neither were there any effects detected of macrophyte vegetation area.

We suggest that constructed wetlands should aim for high invertebrate biomass and species richness. Wetlands should be designed in shapes that maximize shoreline length, which can be further increased by adding islands. In constructed wetlands within agricultural landscapes, controlling alien predators should be implemented to support the duck brood stage.

Introduction

Wetland loss and serious deterioration have led to global waterfowl declines, and for instance in Europe, several duck species are currently classified as Vulnerable or Near Threatened on the Red List (IUCN 2025). Wetlands are on a global scale very important concentration of biodiversity (Gibbs 2000). Even though the value of wetlands is widely recognized, wetland destruction by humans has accelerated during the past decades (Amezaga et al. 2002; Santamaria and Green 2002; Ma et al. 2010; Kingsford et al. 2016; Fluet-Chouinard et al. 2023). Drainage of wetlands, especially for agricultural practices, has occurred all over the world (Millennium Ecosystem Assessment 2005). In boreal forests in northern Europe, millions of hectares of peatlands and other wet forest habitats have been ditched for wood production (Kuusisto et al. 1998). In addition to this direct wetland destruction, climate warming (McMenamin et al. 2008) and over-exploitation of beavers (*Castor* sp.) (Naiman et al. 1988; Nolet and Rosell 1998) have had indirect effects on the amount and distribution of wetlands.

Also, Finnish national duck pair and brood surveys show alarming declining trends for common species (Pöysä et al. 2013; Lehtikoinen 2016; Piha et al. 2025). Changes in water quality and increased predator pressure seem to be driving the trends (Holopainen et al. 2024a). Boreal predator communities have changed due to the introduction and spread of invasive alien predators. For instance, the raccoon dog

(*Nyctereutes procyonoides*) and American mink (*Neogale vison*) have been spreading in Europe (Kauhala and Kowalczyk 2011) and seem to be threatening breeding waterfowl also in Finland (Nummi et al. 2019; Pöysä et al. 2023; Holopainen et al. 2024a; Selonen et al. 2025). Predator communities are found to be affected especially by landscape fragmentation, which has typically increased predator abundance and diversity (Andrén 1995; Pasitschniak-Arts and Messier 1996). This pattern is especially pronounced in fragmented agricultural and forest landscapes, where there are already high numbers of predators from before, such as corvids (Andrén 1992; Roos 2002; Holopainen et al. 2024a, c). For the ducks, nesting near wetlands in agricultural landscape seems to be risky (Higgins 1977). However, even this risky landscape might have safer spots. As suggested by Holopainen et al. (2024b), nesting near a seasonal or constructed wetland might lower the nest predation risk.

Furthermore, food resources (i.e. invertebrate abundance) and habitat structure (e.g. occurrence of islands) are the key characteristics affecting habitat use by duck pairs and broods as well as breeding success (Hill 1984; Nummi and Pöysä 1995a; Cox et al. 1998; Nummi and Hahtola 2008). A large share of the boreal lakes is oligotrophic, meaning that they have a low invertebrate productivity, making them less suitable for brood rearing as compared to eutrophic lakes (Sjöberg et al. 2000; Nummi and Hahtola 2008; Nummi et al. 2013). Various habitat characteristics are shown to influence aquatic invertebrate communities, e.g. macrophyte vegetation, age of wetland and presence of fishes (Thomaz and Cunha, 2010; Ruhí et al. 2012; Nummi et al. 2016; Nummi et al. 2024).

In Finland, constructing wetlands is encouraged to compensate the long-term loss of wetlands and support declining duck populations (Čehovská et al. 2022). Wetlands constructed for waterbirds (including ducks) could have multidisciplinary conservation benefits concerning both fauna and water protection (Kennedy and Mayer 2002; Söderquist et al. 2021; Zhang et al. 2020; Lehikoinen et al. 2017; Kačergytė et al. 2021, 2023; Rawal et al. 2026). Indeed, constructed wetlands have been shown to support higher waterbird species richness in agricultural landscape compared to natural wetlands (Söderquist et al. 2021). In addition, in ducks, constructed wetlands show higher levels of production than average natural boreal lakes, which is related to high invertebrate abundance (Čehovská et al. 2022).

While earlier studies have identified the importance of some habitat characteristics and food web attributes to duck abundances on constructed wetlands (e.g. Danell and Sjöberg 1982; Kačergytė et al. 2021; Čehovská et al. 2022; Rawal et al. 2026), to our knowledge, no studies have combined them all in the same study. In this study, we evaluate the abundance of duck pairs, broods and ducklings (all species pooled together and the most common duck species separately) at the constructed wetlands in relation to aquatic invertebrate abundance, invertebrate species richness, predator abundance and habitat characteristics. Here we studied 44 constructed Finnish wetlands that were created for waterbirds. We hypothesize that the abundance of duck pairs, broods and ducklings are positively associated with higher invertebrate production, shoreline length, agriculture landscape and island availability, and that predator abundance has a negative effect.

Material and methods

We evaluated 11 explanatory variables (Supplementary Table S1.1) representing habitat characteristics, food availability, and predation pressure that may influence a wetland's suitability as a pairing and breeding environment for ducks. These variables were: agricultural habitat, wetland area, islands (a three-level factor = Group 0: 0 islands, Group 1: 1–5 islands, Group 2: > 6 islands), island area, shoreline length (wetland shoreline length combined with islands shoreline length), aquatic vegetation area, wetland age, invertebrate biomass, invertebrate abundance, invertebrate species richness, and a predator index.

Study area

Data for the study were gathered in 2020 from 44 constructed wetlands located in area of seven different counties in southern and eastern Finland (Fig. 1). The studied wetlands are in typical fragmented landscapes, which are a mosaic of managed coniferous and mixed forests of various ages, grazed or cultivated field areas and infrastructure (e.g. human settlement, roads and agricultural land). Constructed wetlands were selected to represent a diverse range in terms of physical characteristics, age, and surrounding landscape. Selected wetlands were distinctly separate entities (e.g. not connected to each other). In cases where separate wetland ponds had a clear connection, e.g. locating very close to each other or they had a direct water connection, these ponds were treated in further analyses as one entity.

Each wetland was expected to hold water for the entire study period, and no construction nor other modification work was done on the wetlands during the year of data collection. No supplementary feeding for ducks was provided, and no birds were introduced to the wetlands during the study or before it.

Duck surveys

Duck survey data were collected from 44 wetlands in 2020, starting each survey round from the southernmost location and ending the survey at the northmost site (Fig. 1).

A pair survey was conducted once (22.4.–15.5.) and brood survey twice (27.5.–18.6.2020, 1.7.–12.7.2020) on each wetland. Brood surveys were conducted twice to have a more comprehensive understanding of broods that were able to use wetland during the whole brood phase. In addition, by repeating brood surveys we had a possibility to track also production of late nesting pairs.

Each duck pair and brood survey included a point count and a round count by foot (Koskimies and Väisänen 1991). Broods were divided into age classes according to Pirkola and Högmänder (1974). For this study, we combined brood observations from both survey rounds. We first took all broods recorded in the first round and then added broods from the second round that, based on duckling age or brood

size, could not have been the same broods already observed earlier. Consequently, the resulting brood count was always greater than or equal to the maximum number recorded in either round. This combined total reflects the brood/duckling situation more realistically than results of individual surveys where e.g. early mortality has not been considered.

We analyzed all duck species pooled together and the most abundant species separately: mallard (*Anas platyrhynchos*), common teal (*Anas crecca*, hereafter teal), common goldeneye (*Bucephala clangula*, hereafter goldeneye) and Eurasian wigeon (*Mareca penelope*, hereafter wigeon).

Habitat data and wetland characteristics

Wetland area, shoreline length (with islands), number of islands, total area of islands and total shoreline of islands were calculated based on the latest aerial and/or satellite images available on Paikkatietoikkuna (2020) or Google Earth Pro (2020) during 2020 for each wetland. For some wetlands (ID: 18, 34 and partially 11, 14; see Supplementary Table S1.3), aerial images were not available because they were only recently created; calculations were then based on field observations. In cases where a wetland was formed of two or more separate ponds, wetland characteristics were determined as a sum of all ponds. In this study “island” was defined as an object at least 1 m² in size, separate from the shoreline and above the water surface. We grouped the number of islands into three categories because some wetlands contained many islands, e.g. wetlands ID 20 had 107 islands and ID 44 had 45 islands.

In our study, we combined the shoreline length of the wetland edges with that of its islands to account for that islands simply increase the amount of suitable habitat for ducks. Thus, in our case, shoreline length represents a composite measure of habitat size, food availability, nesting opportunities, and shelter from predators. Similarly, the grouping variable coding for number of islands here describes habitat quality rather than the amount of added habitat.

Aquatic vegetation area, and percentage of agricultural area around each wetland and wetland age were estimated during the survey. Aquatic vegetation area (the percentage of open-water area covered by emergent vegetation) at each wetland was estimated by eye from the entire open water area. For wetland complexes consisting of multiple basins, the aquatic vegetation area was calculated across basins to represent the entire site. Several wetlands were newly constructed and had not yet developed vegetation, whereas others supported either a diverse assemblage of plant species or only a few dominant taxa. In some cases, vegetation was heavily dominated by a single aggressively spreading species, e.g. the common reed (*Phragmites australis*).

Agricultural habitat was expressed as the area in km² of agricultural land in a buffer zone with a radius of 1 km of each wetland. Wetland age in years was determined by directly asking from landowners or by using other open sources (e.g. municipalities' reports).

Invertebrate data

To evaluate the invertebrate food abundance at constructed wetlands, we carried out aquatic invertebrate trapping in all 44 wetland sites during the first brood surveys. In locations where it wasn't possible to carry out trapping during first brood surveys due to cattle grazing, supplementary trappings were conducted during the second brood surveys (ID: 28 and 34; see Supplementary Table S1.3). One wetland site (ID 26) was excluded from the analysis, as it wasn't possible to carry out the invertebrate trapping at that location.

Four activity traps were used to collect samples for two days (48 hours). Activity traps were made of one-litre glass jars with plastic funnels with 10 cm openings at the wide end and 2,3 cm at the narrow end described by Hyvönen and Nummi (2000). Activity traps were placed close to the shoreline at a water depth of 25–30 cm. When emptying the content was passed through a 1 mm sieve and gently washed out. The content of each trap was sorted, and water invertebrates were classified into taxons and size categories following the classification by Nudds & Bowlby (1984). However, some invertebrates did not fit into predefined size categories, and in those situations modified size categories were used. To get a comprehensive view of invertebrate food abundance at constructed wetlands, we used the following invertebrate variables: invertebrate biomass index and invertebrates' species richness (number of different taxa found at each wetland site). For invertebrate biomass index, the number of all invertebrate individuals in each taxon were multiplied by the mean size category (mm) defined by Nudds and Bowlby (1984), then summed, and divided by the number of traps used and by number of days that traps were at the sites. The resulting unit of the biomass index is hence number of individuals $\times$ mean size (mm) $\times$ trap⁻¹ $\times$ trapday⁻¹.

Predator data

In our study areas in southern and eastern Finland the raccoon dog, pine marten (*Martes martes*), red fox (*Vulpes vulpes*), Eurasian badger (*Meles meles*) and American mink are the most common mammal nest predators (Holopainen et al. 2020). The relative abundance of predator populations around the study wetlands was evaluated by using wildlife cameras with signposts (see method for more details in Krüger et al. 2018). A commercial lure Gray Ambush (J.R. and Sons, Monroeville, OH, USA, made from grey fox (*Urocyon cinereoargenteus*) glands) were used to attract mammal predators to the area within the clear camera view. We dipped around 20 cm long wooden sticks in the lure, and additionally placed lure on a stone, providing a fixed source of scent in case predators carried the sticks out of the camera's view. We placed a signpost in the middle of the camera's view. We placed two camera traps in each of the study wetlands, one on each side near the wetland shore. The cameras were active for the four-day study period and responded to movement, taking three pictures in a row followed by a one-minute pause. It wasn't possible to use cameras with signposts at one wetland site (ID 28). Due to missing data, this wetland was excluded from the analysis. The signpost experiment was carried out in May and June 2020.

We calculated a predator abundance index for each constructed wetland as follows. All pictures from a four-day study period were reviewed (Supplementary Table S1.2). Every predator observation which occurred 30 minutes apart from earlier observation was counted by species and by number of individuals in the picture. The sum of all predator observations was divided by the number of cameras and by the number of days the cameras were at the wetland.

Statistical analysis

Initial data exploration involved 11 explanatory variables: agricultural habitat (AgriHabitatKm2), wetland area (AreaHa), islands (IslandGroup; three-level factor variable), island area (IslandAreaHa), shoreline length (ShoreCombined), aquatic vegetation area (AquaticVegetationArea), age of wetland (AgeIn2020), invertebrate biomass (InvtBiomass), invertebrate number (InvtNumber), invertebrate species richness (InvtSpeciesRichness) and predator index (PredatorIndex). When two variables were strongly correlated, defined as $|r| > 0.6$, we kept the variable which we thought had larger ecological relevance and excluded the other from further analyses (Supplementary Table S2). Consequently, we omitted from our analysis wetland area due to its correlation with shoreline length; island area due to its correlation with wetland area and shoreline length; year of wetland creation due to its correlation with wetland age; and number of invertebrates due to its correlation with invertebrate biomass. Hence, we explained duck abundances with eight variables (see Supplementary Table S1.3 for wetland-specific values of the eight explanatory variables): agricultural habitat (AgriHabitatKm2), shoreline length (ShoreCombined), islands (IslandGroup; factor variable), aquatic vegetation area (AquaticVegetationArea), age of wetlands (AgeIn2020), invertebrate species richness (InvtSpeciesRichness), invertebrate biomass index (InvtBiomass) and predator index (PredatorIndex).

We investigated in total 14 response variables: number of duck broods, number of ducklings, number of duck pairs; mallard broods, ducklings, pairs; teal broods, ducklings, pairs; goldeneye broods, ducklings, pairs; wigeon broods and pairs. Wigeon ducklings were included only in the total duckling count but were not analyzed as a separate response due to very unbalanced and zero inflated distribution preventing the models from converging. Statistical analyses were performed in R version 4.3.2 (R Core Team 2024) using the packages DHARMA (Hartig 2024), ggplot2 (Wickham 2016), GGally (Schloerke et al. 2024), glmmTMB (Brooks et al. 2017), glmulti (Calcagno 2020), leaps (Lumley 2024), MASS (Venables and Ripley 2002), MuMIn (Bartoń 2024), pscl (Jackman 2020), and rJava (Urbanek 2024). Because our duck data were overdispersed, we applied negative binomial generalized linear models (GLM) with a log link function. The models were fitted using function glmmTMB, in the package glmmTMB; without any random effects. We performed exhaustive screening of candidate model sets based on all combinations of the main terms, with no more than four variables in each model to take into account our limited number of sampled sites ($N = 42$) (Burnham and Anderson 2002). We also provide the null model (intercept-only). This resulted in 163 candidate models for each of our fourteen dependent variables, including the null model (intercept only). Model averaging was then performed across the full set of candidate models to reduce the influence of uninformative parameters (Arnold 2010). From these, we identified the subset of models with $\Delta AICc < 2$ (hereafter “best models”) and flagged the ones that

contained uninformative parameters (Supplementary Table S3). Parameter estimates, standard errors, and 95% confidence intervals were derived from model averaging across all candidate models (Supplementary Table S4). In addition, we calculated the relative importance of each predictor by summing its Akaike weights (based on ΔAIC_c) across all models in which it appeared; higher summed weights indicate greater importance relative to the other variables considered (Fig. 2). Interpretation of the results was based on the conditional model-averaged coefficients (Supplementary Table S4).

Results

Duck survey

The 44 constructed wetlands (Fig. 1) supported nine duck species during the breeding season. Among these species, seven were observed with broods (Table 1): mallard, teal, goldeneye, wigeon, shoveler (*Spatula clypeata*), pintail (*Anas acuta*), and tufted duck (*Aythya fuligula*). In addition, common pochard (*Aythya ferina*) and garganey (*Spatula querquedula*) were present only as pairs and were therefore not included into the analyses. However, it is possible that they tried nesting but failed; therefore, no brood observations.

Table 1

Total pair, brood and duckling counts, their averages (avg.) per wetland, standard deviation (SD), and average brood size at the 44 studied constructed wetlands

Pairs tot.	Mallard	Teal	Goldeneye	Wigeon	Shoveler	Pintail	Tufted duck
Pairs avg.	90	106	73	26	12	5	12
SD	2.05	2.41	1.66	0.59	0.27	0.11	0.27
	1.97	3.03	1.74	1.07	2.24	0.43	1.74
Broods tot.	45	66	98	23	3	4	4
Broods avg.	1.02	1.5	2.23	0.52	0.07	0.09	0.09
SD	2.05	2.60	2.49	1.08	0.00	0.00	0.47
Ducklings tot.	251	367	462	76	19	14	16
Ducklings avg.	5.70	8.34	10.50	1.73	0.43	0.32	0.36
SD	11.67	15.01	15.29	3.70	3.86	1.66	2.36
Average brood size (ducklings/broods)	5.86	5.60	3.95	3.60	6.33	3.50	4.17
SD	2.65	2.73	2.11	2.29	3.86	1.66	2.09

Duck pairs

Reaching 95% evidence weight required 30 models for duck pairs overall, and 97, 101, 59, and 94 models for mallard, teal, goldeneye, and wigeon pairs respectively, indicating the support was spread over many alternatives.

Results from the negative binomial models explaining the number of duck pairs at constructed wetlands identified four best models, all of which included shoreline length, the predictor with the highest importance (Supplementary material Table S3, Fig. 2). The top-ranked model contained, in addition to shoreline length, invertebrate biomass and invertebrate species richness, being clearly superior to the null model (intercept-only; $\Delta\text{AICc} = 15.90$, weight = 0.00). Based on model averaging the total number of duck pairs was positively associated with the shoreline length and the invertebrate species richness (Supplementary material Table S4).

Eight best models explaining mallard pair number were identified, having agricultural habitat as the most consistent and important predictor (Supplementary material Table S3, Fig. 2). The two top-ranked models with almost identical AICc values (165.14 and 165.15) and equal weights (0.06) contained, in addition, either the age of wetland or shoreline length. The null model was not within the best-fitting models ($\Delta\text{AICc} = 2.50$, weight = 0.02), but was quite close, indicating weak results. Mallard pairs were more abundant at wetlands embedded in more agricultural landscapes in the model averaged results, while other explanatory variables had only weak support (Supplementary material Table S4).

Model selection explaining the number of teal pairs identified three best models, all of which included predator index and shoreline length (Supplementary material Table S3, Fig. 2), which performed clearly better than the null model ($\Delta\text{AICc} = 4.41$, weight = 0.01). The model averaged coefficients revealed that teal pairs were positively associated with shoreline length, while negatively associated with the predator index (Supplementary material Table S4).

Model selection for goldeneye pairs identified four best models, in which the most consistent predictors were invertebrate biomass and shoreline length (Supplementary material Table S3, Fig. 2), being clearly superior to the null model ($\Delta\text{AICc} = 10.36$, weight = 0.00). Goldeneye pairs were positively associated with shoreline length and invertebrate biomass in the model averaged results (Supplementary material Table S4).

In case of wigeon pair model selection, seven best models were identified. All supported models included shoreline length, this being the parameter with the highest importance (Supplementary material Table S3, Fig. 2). The best model with the lowest AICc included variables age of wetlands, aquatic vegetation area, invertebrate species richness and shoreline length, and provided a clearly better explanation of the data than the null model ($\Delta\text{AICc} = 4.90$, weight = 0.01). Based on model averaging, wigeon pairs were positively associated with the shoreline length (Supplementary material Table S4).

Duck broods

For duck broods, 40 models were needed to reach 95% evidence weight, and mallard, teal, goldeneye, and wigeon broods required 43, 124, 26, and 110 models respectively, indicating considerable model

selection uncertainty.

The three best models explaining total duck brood abundance included agricultural habitat and shoreline length, together with either invertebrate species richness or invertebrate biomass (Supplementary material Table S3, Fig. 2). All three models performed substantially better than the null model ($\Delta AICc = 15.22$, weight = 0.00). The model averaged coefficients revealed that duck brood abundance increased with shoreline length and invertebrate species richness, while it declined in the agricultural habitat. Age of wetlands, predator index, islands and aquatic vegetation area did not show strong relationships with brood abundance (Supplementary material Table S4).

Mallard brood models contained five best models, containing invertebrate species richness and shoreline length, with weaker and less consistent contributions from predator index, agricultural habitat and invertebrate biomass (Supplementary material Table S3, Fig. 2), and provided a clearly better explanation of the data than the null model ($\Delta AICc = 43.49$, weight = 0.00). Mallard broods were positively associated with shoreline length and invertebrate species richness in the model averaged results (Supplementary material Table S4).

Model selection for teal broods did not reveal any clearly supported model. There were identified 22 best models, including also the null model ($\Delta AICc = 1.87$, weight = 0.01) (Supplementary material Table S3). Consequently, teal broods were not associated with any of our explanatory variables in the model averaged results (Supplementary material Table S4, Fig. 2).

Model selection for goldeneye broods revealed three best models, all containing the invertebrate biomass and shoreline length as explanatory variables (Supplementary material Table S3, Fig. 2), being clearly superior to the null model ($\Delta AICc = 15.20$, weight = 0.00). Based on model averaged coefficients, goldeneye broods were positively correlated with the shoreline length and the invertebrate biomass while negatively associated with the agriculture habitat (Supplementary material Table S4).

All nine wigeon-brood best models showed very low model weights (0.02–0.06), implying minimal effect of our predictors (Supplementary material Table S3, Fig. 2). The null model was not included in the top selection, but it still received some weight ($\Delta AICc = 3.46$, weight = 0.01). In the model averaged results, the abundance of wigeon broods could not be explained by any of our variables (Supplementary material Table S4).

Ducklings

For ducklings, 57 models reached 95% evidence weight, and mallard, teal, and goldeneye ducklings required 55, 109, and 99 models respectively, reflecting that the evidence was spread across many competing models.

Model selection for all ducklings identified five best models, from which two had clearly better fit, both containing invertebrate biomass and shoreline length as explanatory variables (Supplementary material Table S3, Fig. 2), which performed substantially better than the null model ($\Delta AICc = 10.33$, weight = 0.00).

The total number of ducklings was based on model averaging positively correlated with the shoreline length (Supplementary material Table S4).

Three best models were identified for mallard ducklings, with two of them being nearly equivalent in performance. Shoreline length was the most important predictor of mallard duckling abundance being included in all three models with contributions from wetland age and aquatic vegetation area (Supplementary material Table S3, Fig. 2). The best model was clearly superior to the null ($\Delta AICc = 5.59$, weight = 0.01). Based on model averaged coefficients, mallard ducklings were positively associated with the shoreline length (Supplementary material Table S4).

Model selection for teal ducklings did not detect clear support for any of our explanatory variables. There were fourteen best models, and the null model was the top-ranked model ($AICc = 230.80$, weight = 0.04). That indicates that the considered environmental variables had no meaningful explanatory power for teal ducklings (Supplementary material Table S3 and S4, Fig. 2).

Goldeneye duckling model selection resulted in the nine best models, shoreline length and invertebrate biomass being the most consistent explanatory variables followed by invertebrate species richness and agricultural habitat (Supplementary material Table S3, Fig. 2), which performed substantially better than the null model ($\Delta AICc = 4.52$, weight = 0.01). However, based on model averaged coefficients, none of our explanatory variables explained the abundance of goldeneye ducklings (Supplementary material Table S4).

Discussion

The total shoreline length and food resources (invertebrate biomass and species richness) stand out as the main drivers of duck breeding parameters in boreal constructed wetlands. Hence, they were the most important factors explaining the total number (pooled over species) of duck pairs, broods and ducklings, and they often received high weights at the species level, too. High percent of agricultural surroundings around the studied wetlands had a positive effect on mallard pairs, while the effect was negative on duck broods and on species level, on goldeneye abundance at wetlands.

Shoreline length is often one of the primary habitat features associated with higher duck abundance (Bartzen et al. 2017; Čehovská et al. 2022). It reflects wetland size, larger wetlands generally supporting more ducks (Elmberg et al. 1994; Sebastián-González and Green 2014; Rawal et al. 2026), but the shoreline length also indicates feeding opportunities, especially for dabbling species such as mallards and teals that forage extensively for invertebrates along shallow shore zones (Pöysä 1983; Monda and Ratti 1988; Nummi et al. 1994; Cooper and Anderson 1996).

Foraging conditions greatly affect the reproductive success of ducks. Breeding duck females consume plentiful aquatic invertebrates (Krapu 1974; Swanson et al. 1985), and ducklings feed almost exclusively on emerging insects and other aquatic invertebrates (Perret 1962; Reinecke 1979; Nummi 1985). Food availability affects duckling growth rate and survival (Cox et al. 1998; Sjöberg et al. 2000; Marteau et al.

2025). It is therefore highly important for brood rearing females to select habitats with high amount of invertebrate food (Nummi et al. 2013). As highlighted in another study (Cooper and Anderson 1996), our results confirm that invertebrates are important driving factors in duck habitat use also in constructed wetlands. More specifically, we found out that both invertebrate biomass and invertebrate species richness were crucial factors affecting abundances of pairs, broods and ducklings in our constructed wetlands. We observed the effect both with the data pooled from different species and at the species level. Invertebrate biomass occurred among the top three tested parameters for goldeneye pairs, broods and ducklings, indicating that these species prefer wetlands with especially abundant food resources. On the other hand, invertebrate species richness was important for mallard and wigeon broods, in addition to teal pairs. Duck broods of different species search for different invertebrate taxa, e.g. teal ducklings search for small emerging insects while goldeneye ducklings search for aquatic invertebrates in the water column and large emerging insects (Collias and Collias 1963; Sugden 1973; Nummi et al. 2013). Invertebrate species richness may thus support more duck species, but it can also be beneficial for ducklings through the summer season. Ducklings use different kinds of invertebrates during different stages of their development (Chura 1961; Perret 1962; Sugden 1973).

Agricultural lands can be more invertebrate-rich. That is, nutrients from agricultural fields and cattle grazing increase the abundance of nutrient-tolerant invertebrate species (Campbell et al. 2009) but do not reach hypertrophic levels that are unfavorable for most aquatic organisms (Hansson et al. 2005). For example, Liston et al. (2008) found that macroinvertebrate biomass in oligotrophic waters initially increased with eutrophication, up to the point where extreme nutrient levels caused the loss of periphyton mats. Nevertheless, we do not have data about nutrients in our constructed wetlands, and we found only weak intercorrelation between agricultural land and invertebrate biomass (-0.12) or invertebrate species richness (0.02). In the boreal zone, agriculture lands usually support more ducks than e.g. forest wetlands, because boreal lakes are naturally oligotrophic (Holopainen et al. 2024b).

In our study, we found mixed responses of breeding ducks to agricultural habitat. It was the most important parameter for mallard pairs which were positively associated with the amount of agricultural land surrounding wetlands. This parameter ranked among the top three parameters for duck broods, goldeneye pairs and broods but on the contrary, their association with the agricultural habitat was negative. Agricultural lands tend to have higher avian and mammal predation rate than forest habitats (Elmberg and Gunnarsson 2007; Gunnarsson and Elmberg 2008; Holopainen et al. 2024b), which could explain lower brood abundance. As Elmberg and Gunnarsson (2007) noted, agricultural wetlands attract duck pairs potentially due to abundant food resources, but nest predation rates are on the other hand higher there, compared to forested wetlands. Also, the vegetation structure of the agricultural wetlands may have negative effects. Eutrophication typically leads to development of monoculture of plants e.g. stands consisting mainly of *Phragmites* sp. that are not preferred by ducks (Nummi and Pöysä 1995b; Viksne et al. 2005; Robichaud and Rooney 2017). Concerning goldeneye, in cultivated landscape there might be a lack of suitable trees with holes needed for cavity nesting ducks (Pöysä and Pöysä, 2002).

Age of wetlands was the second most important parameter for mallard and wigeon pairs, having positive association with their abundance. In a larger dataset of constructed wetlands in Finland (containing also those with other purpose than enhancing biodiversity), Rawal et al. (2026) found that in newly created wetlands duck pairs and broods gradually increased, then peaked between 4 to 7 years, and after that started to decline. That study did not include information on invertebrates, but similar timing of duck peak was observed also in other studies which showed corresponding trend of ducks with the succession of aquatic invertebrates (Danell and Sjöberg 1982; Sjöberg and Danell 1983; Nummi et al. 1999). However, none of these studies included information on fish which are known to compete with ducks for invertebrates (Hill et al. 1987; Elmberg et al. 2010; Nummi et al. 2016). One of the reasons presumed to cause a decrease in both invertebrates and ducks over time is the depletion of nutrients (Murkin 1989). The amount of nutrients is high in the initial phase from inundated vegetation (Fredrickson and Reid 1988; Nummi 1989; Coccia et al. 2016). In our study, we have not found a declining trend of breeding duck abundances over time after wetlands construction. It could be that our sample size was relatively small, containing also some very young wetlands. It could also be that nutrient exhaustion might be mitigated by luxurious vegetation structures that can provide food and shelter for invertebrates (see Murkin 1989; Downing 1991). All our wetlands were also within agricultural landscape, thus potentially getting nutrient flow from the fields.

Nesting and brood-rearing females often face a habitat-selection trade-off between areas with abundant food and those with lower predation risk (Bloom et al. 2013; Holopainen et al. 2024b). Predator index received high support for teal pairs and teal and mallard broods which were negatively associated with increased mammalian predation pressure. Many predators may affect reproduction in several ways, for instance directly predating nests or duckling. European and North American studies have shown that duck nest survival has improved when mammalian predators were removed (Duebbert and Lokemoen 1980; Garrettson and Rohwer 2001; Nummi et al. 2019; Jaatinen et al. 2022). Increased survival on predator-removed sites was observed also in mallard ducklings (Pearse and Ratti 2004).

The aquatic vegetation area was among the least important explanatory variables in our analysis. Aquatic vegetation is generally expected to benefit ducks by providing multiple services, including shelter from predators, as well as nesting and foraging opportunities (Batt 1992; Nummi and Pöysä 1993; Keller et al. 2020). Adult ducks and ducklings can forage emerging insects on plant surfaces (King and Wrubleski 1998; Nummi et al. 2000) and based on the duck feeding niche also plants themselves (e.g. Sugden 1973; Fredrickson and Reid 1988). Moreover, wetlands with diverse macrophyte communities typically support higher invertebrate richness and abundance (Downing 1991; Bazzanti et al. 2008). In our study, the aquatic vegetation area appeared as the third most important variable in the models explaining wigeon pair abundance, the effect being positive. This finding corresponds to the fact that wigeons have a more herbivorous diet than many other duck species (Cramp et al. 1977; Dessborn et al. 2011) and wigeon has been observed to choose wetlands due to their vegetation structure (Nummi et al. 2013).

Unlike hypothesized, we found that the island group (representing the number of islands) had a surprisingly weak effect on breeding duck abundance, beyond the effect of added shoreline, which was most often already included in the best model as a separate variable. We expected a stronger response because islands typically have higher nest success due to lower predation pressure compared to mainland sites (Hill 1984; Holopainen et al. 2015). Islands are often recommended in wetland construction for this reason (Nummi et al. 2024). However, the island group emerged as the third most important variable only in models explaining wigeon brood abundance. All in all, this result may also not be totally surprising, because goldeneye nests in cavities are not established at the islands, while teal and mallard are flexible nesters, that can nest even far away from the wetlands. Thus, wigeon probably uses islands for nesting more than the other species, explaining why it appeared to be the only species benefiting from island groups.

Declarations

Funding

The field work was funded by the Ministry of Agriculture and Forestry of Finland through the SOTKA Luke project (ref: VN/7370/2020-MMM-9). The contribution of MN was funded by the Societas pro Fauna et Flora Fennica. The contributions of CA and AL were funded by the Research Council of Finland (grant numbers 333400 and 357200, respectively).

Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contribution

Contributor roles are described according to CRediT– Contributor Roles Taxonomy (niso.org) as follows: Conceptualization V-MV, SH, CA; Data curation ST, V-MV, MN, SH; Formal analysis MN, SH, CA; Funding acquisition AL, ST, V-MV, MN; Investigation V-MV, ST, AL; Methodology ST, V-MV, MN, SH, CA; Supervision SH, CA; Writing – original draft MN, ST, SH, V-MV, CA; Writing–review and editing MN, ST, SH, V-MV, CA, AL.

Acknowledgement

We thank Hannu Pöysä for providing valuable comments that substantially improved this manuscript.

Data Availability

The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

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Figures

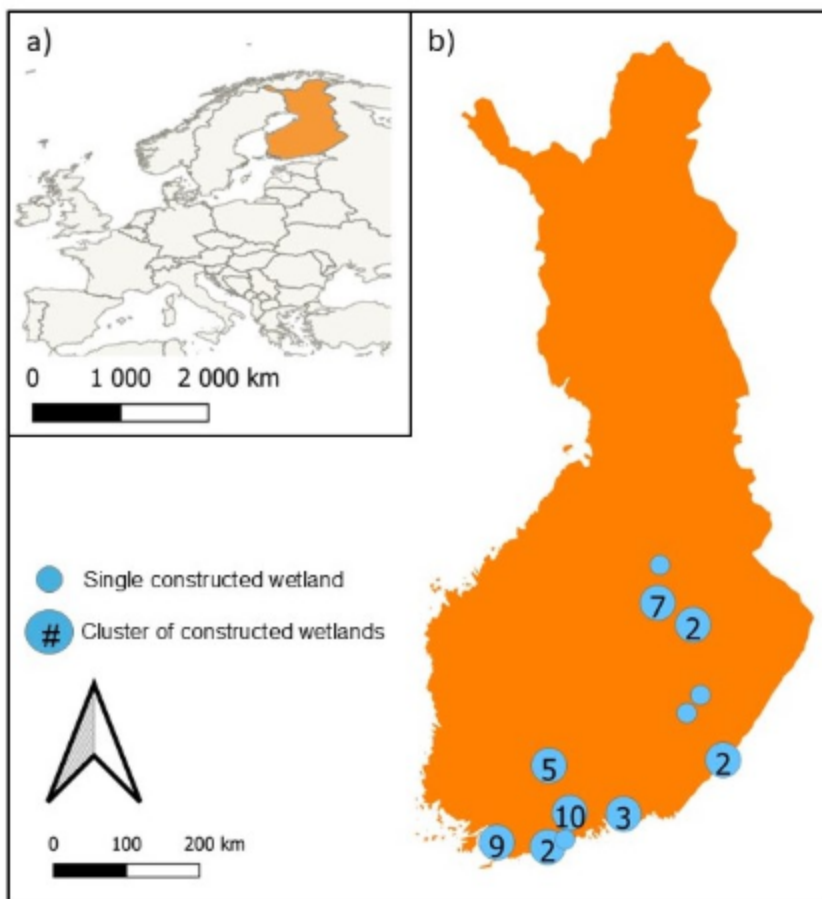


Figure 1

a) Geographical position of Finland within Europe b) location of the 44 studied constructed wetlands within Finland. For clusters with several wetlands close to each other, the number of wetlands is displayed inside the blue circles

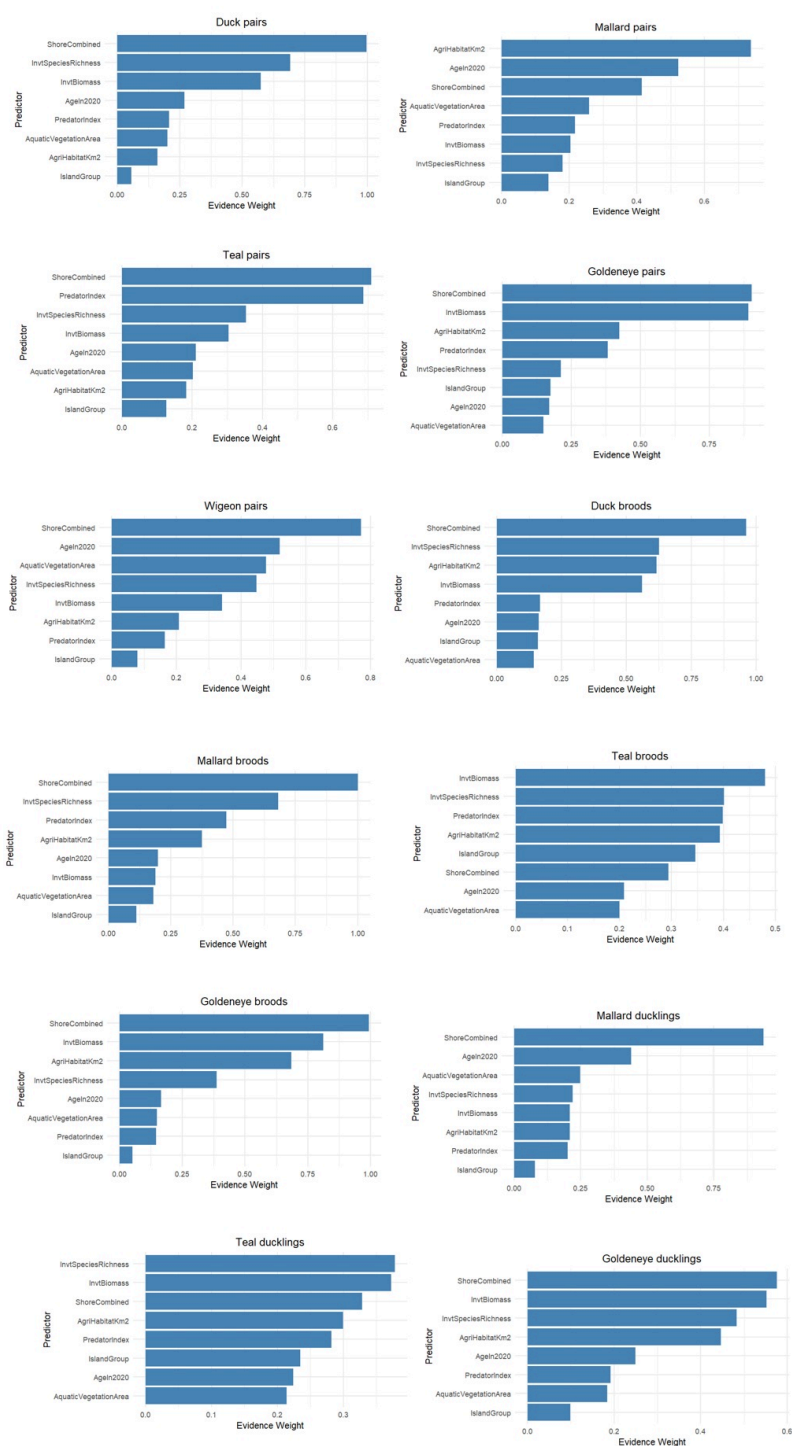


Figure 2

The relative importance of environmental variables to explain the abundance of duck breeding pairs, broods and ducklings including species -specific responses of mallard, teal, goldeneye, and wigeon at 42 studied constructed wetlands. All values represent conditional model-averaged importance weights.

AgeIn2020 = the age of wetland in the year 2020, AgriHabitatKm2 = the area in km² of agricultural land in a buffer zone with a radius of 1 km of each study wetland, AquaticVegetationArea = % of water surface

covered by vegetation , InvtBiomass = biomass index (the sum of all invertebrate individuals in each taxon multiplied by the mean values of the size categories (Nudds and Bowlby 1984) divided by the number of traps used and by number of days that traps were at sites), InvtSpeciesRichness = number of different taxa found at each study wetland, IslandGroup = Group 0: 0 islands, Group 1: 1–5 islands, Group 2: > 6 islands, PredatorIndex = predator/cametraps/day, ShoreCombined = wetland shoreline length combined with islands shoreline length (km). Higher weights indicate stronger support for each predictor across the model set.

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