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ORIGINAL ARTICLE

Compensating freshwater habitat loss—duck productivity and food resources in man-made wetlands

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Abstract
The number of wetlands in Europe decreased by more than 60% by the 1990s compared with the beginning of the twentieth century. Man-made wetlands may be an effective way to compensate for the loss and degradation of freshwater ecosystems. This loss impacts the populations of declining duck species, partly due to a lack of suitable breeding opportunities. In this study, we evaluated duck productivity and invertebrate abundance in 13 man-made Finnish wetlands that were created for waterbirds. Our findings revealed that man-made wetlands have higher duck production than average natural boreal lakes. High invertebrate levels were a key factor that positively correlated with duck pair density, brood density, duckling density of the common teal (*Anas crecca*), and duck density during the post-breeding period. Our results suggest that man-made wetlands are a useful tool for increasing duck productivity. For upholding this status in the long term, appropriate management should involve maintaining sufficient invertebrate levels.

Keywords Aquatic invertebrates · *Anas crecca* · Wetland management

Introduction

Freshwater habitats are considered the most endangered ecosystems worldwide (Dudgeon et al. 2006; Darwall et al. 2009), facing more rapid declines in biodiversity than terrestrial and marine ecosystems (Millennium Ecosystem Assessment 2005; Darwall et al. 2009; Collen et al. 2014). Concurrently, wetlands are ranked the most valuable ecosystems in the biosphere, providing more than a quarter of the total estimated ecosystem services despite globally covering only 1.1% of the biosphere surface (Costanza et al. 2014). However, over 70% of these ecosystems have already been seriously deteriorated (Kingsford et al. 2016), with overexploitation, water pollution, flow modification, habitat destruction or degradation, and invasion by exotic species being the main identified factors causing deterioration (Dudgeon et al. 2006; Junk et al. 2013; Reid et al. 2018). The transformation of wetlands to agricultural utilization and forestry purposes, urbanization, or industry and transport are among the major causes for degradation and habitat loss (Kingsford et al. 2016). Mainly for these reasons, the number of wetlands in Europe decreased by more than 60% by the 1990s compared with the beginning of the twentieth century, and this number is still declining (Amezaga et al. 2002). The problem is caused not only by intentional draining but also loss due to current climate change. Higher temperatures and a decrease in precipitation cause alterations (Holopainen et al. 2014a) not only in water levels but also in water chemistry (Čížková et al. 2013).

Wetlands are important for many organism groups, e.g., invertebrates, birds, and mammals (Gibbs 1993, 2000; Guareschi et al. 2020), which provide various ecosystem services (Mitsch et al. 2015). Natural wetlands are not the only sources of biodiversity, as man-made wetlands are also widely used by organisms (Danell and Sjöberg 1982; Wahlroos et al. 2015; Porte and Gupta 2018; Hessen et al. 2019). Waterbirds are an important group of wetland organisms, as they are valuable providers of ecosystem services (Green and Elmberg 2014) and useful indicators of wetland quality (Boere et al. 2006; Green and Elmberg 2014). Ducks are also important quarry species (Holopainen et al. 2018).

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During recent decades, many duck populations have faced declines in Europe. These include the common pochard (*Aythya ferina*), common teal (*Anas crecca,* hereafter teal), Eurasian wigeon (*Mareca penelope*, hereafter wigeon), northern pintail (*Anas acuta*), and garganey (*Spatula querquedula*) (Holopainen et al. 2018). Numerous reasons lie behind these declines, including land-use changes leading to the deterioration of breeding ground habitats (Hilli-Lukkarinen et al. 2011; Arzel et al. 2015; Lehikoinen et al. 2017; Zhao et al. 2019) and high predation caused by alien predators (Nummi et al. 2019a; Pöysä et al. 2019a; Brzeziński et al. 2020; Holopainen et al. 2021). Ducks in the boreal zone were previously believed to be declining particularly in eutrophic lakes (Lehikoinen et al. 2016), but recent studies reveal that oligotrophic lakes also show major population declines (Pöysä et al. 2019b).

Duck presence in wetlands also reflects food resource statuses at the sites. Ducks require high invertebrate levels, especially during the breeding season. Larger pair numbers were present in food-rich lakes (Arzel et al. 2015), and teal broods showed a preference for areas flooded by beavers (*Castor canadensis*), as these areas are rich in invertebrates (Nummi and Hahtola 2008). Other studies revealed that the habitat use by common goldeneye (*Bucephala clangula*, hereafter goldeneye), teal, and mallard (*Anas platyrhynchos*) broods were related to invertebrate prey levels (Väänänen et al. 2012; Nummi et al. 2013; Holopainen et al. 2014b). Small ducklings require large invertebrate numbers (Winfield and Winfield 1994) found on the water surface or on emergent vegetation (King and Wrubleski 1998; Nummi et al. 2000). Food abundance also plays a key role because it influences duckling survival (Gunnarsson et al. 2004). However, the high food requirements of ducklings imply that many wetlands, especially in the boreal zone, may not be suitable habitats for ducks (Sjöberg et al. 2000).

Wetland quantity is not an issue in the European boreal zone, as ponds and lakes number in the hundreds of thousands. However, only a part of boreal ponds and lakes are suitable for duck broods for the abovementioned reasons (Nummi and Pöysä 1995a; Sjöberg et al. 2000), and high-quality and species-rich sites have been declining more rapidly over the past years compared with low-quality areas. For example, 4.7 million hectares of natural mires have been drained in Finland to increase forest growth (Aapala and Lappalainen 1998), and approximately 3000 wetlands were drained, or their water levels were significantly lowered, to gain land for agricultural use in the past two hundred years (Kuusisto et al. 1998). A water level drop leads to a loss of flooded shore meadows and enhances the overgrowth of the shoreline vegetation, which consequently causes a lack of habitats that are important for many waterbird species (Wahlström et al. 1996). A productivity decrease in these sites is another negative impact connected with the water level drop and with changes in the littoral zone, as boreal lakes profit from inundations that bring nutrients to the water from the surrounding landscape (Larmola et al. 2004). Recently, growing interest has focused on creating man-made wetlands for enhancing waterbird populations and aquatic biodiversity in general (Céréghino et al. 2007; Ruhí et al. 2013; Nummi and Holopainen 2020; Rannap et al. 2020). For example, a recent LIFE+project aiming to create man-made wetlands for waterbirds has been implemented in Finland https://www.slideshare.net/Riistakeskus/laymanrapo rtti-layman-report.

Man-made wetlands have been studied globally (Murillo-Pacheco et al. 2018; Porte and Gupta 2018; Hessen et al. 2019). Most European studies concerning ducks have been executed in fishpond habitats in Central Europe (e.g., Albrecht et al. 2000; Musil 2000; Haas et al. 2007). Only a few studies have been conducted that examine the importance of man-made wetlands as boreal breeding grounds, and most of these study designs have incorporated only one pond (Danell and Sjöberg 1982; Sjöberg and Danell 1983; Nummi 1989, 1992; but see Kačergytėet al. 2021).

Here, our aim is to gain a general picture of duck production in man-made wetlands. The wetlands used in our study were created in 2008, with the aim of increasing biodiversity and duck production in oligotrophic boreal forest and peatland areas. The wetlands were monitored for four years after their establishment. We evaluated duck productivity in our study wetlands by comparing them with typical boreal wetlands. We are aware that the study wetlands were created some time ago; however, we do not believe that this affects the processes we are interested in. We will compare duck productivity in our study wetlands during 2008–2011 with boreal wetlands in southern and eastern Finland during 1989–1994 (Nummi and Pöysä 1997a). Our comparisons are conservative according to duck population trends (Holopainen et al. 2018). Moreover, we refer to studies from different time periods (prior to, concurrent with, and more recent than our study) that are relevant to our study. We gathered as much information as possible to evaluate our findings and to provide a comprehensive perspective on the issue of wetland creation for waterbirds.

Based on earlier studies, we predict higher duck productivity and brood/duckling occurrence on lakes with higher invertebrate abundance. We hypothesize that food availability for ducks will be the key determining factor influencing duck productivity and that other environmental conditions, such as macrophyte vegetation cover, will have less of an effect on breeding ducks.

Methods

Study area

Our study wetlands were built within the framework of the "Riistan elinympäristöjen aktiivinen hoito" (REAH) project (i.e., "Active game bird habitat management"), with the target of increasing general biodiversity factors and waterbird productivity in Finland. For this reason, the sites are not intended to produce large quantities of fish, but some fish are present, nonetheless. Fish compete with ducks for invertebrate prey (Anderson 1981; Nummi et al. 2016). As we are interested in duck productivity, we also evaluate the invertebrate levels available for ducks.

Our study incorporated 13 man-made wetlands (Table 1, Fig. 1): 7 wetlands (Saarikko, southern Kirstinkorpi E. and northern Kirstinkorpi P., Kamulanpuro, Orastinsuo Länsiallas, Orastinsuo Väliallas, Orastinsuo Itäallas) were established in 2008 and monitored during 2008–2011, while 6 wetlands (Haarajärvi, Kattilapuro, Varispuro, Lippi, Paloharju, Rypyharju) were established in 2009 and monitored during 2009–2011. The individual lakes differ in size, structure, and water nutrient levels. Saarikko, Haarajärvi, Lippi, Kamulanpuro, and Kattilapuro were flooded by beavers (*Castor canadensis*) in the past. Saarikko is a relatively luxuriant boreal wetland (situated in a fairly open landscape), while the other post-beaver lakes are originally oligotrophic. Other barren lakes include Varispuro, which is a small pond with islands, Paloharju, and Rypyharju. Orastinsuo-Länsiallas, Väliallas, Itäallas, Paloharju, and Rypyharju were constructed on peatland. The Orastinsuo wetlands consist of three interconnected lakes constructed on former peat extraction sites. Kirstinkorpi S. and N. are quite small compared with the average size of the study wetlands. All our study wetlands are located in forest or peatland habitats.

Duck data

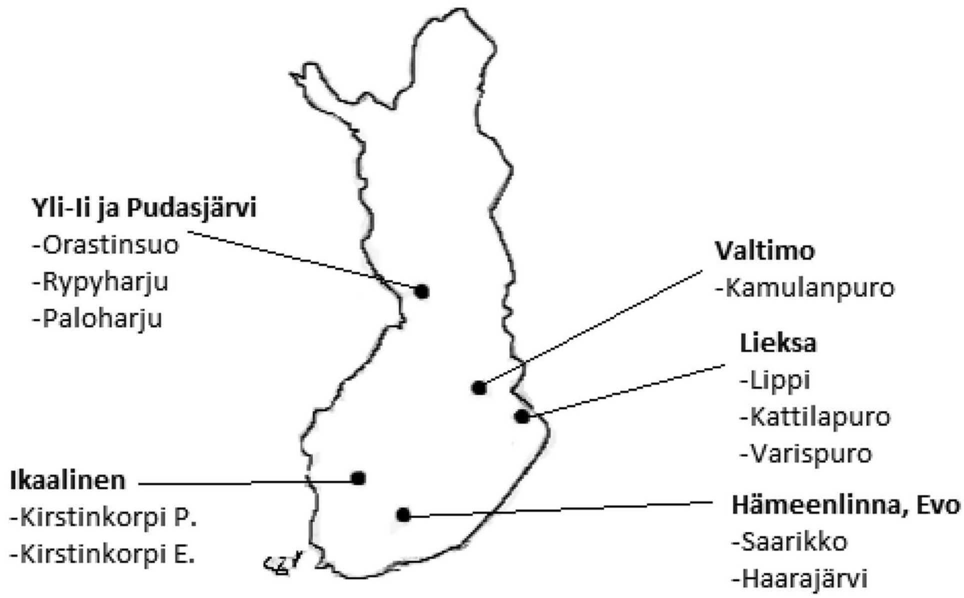
Ducks were monitored from May to August. Eight surveys (two per month) were performed for each wetland using both point and round surveys (see details in Koskimies and Väisänen 1991). Surveys could not be conducted at certain wetlands during certain years due to drought conditions. Surveys around the waterbodies were necessary because of the abundant littoral vegetation surrounding some of the wetlands, leading to poor visibility across the wetland from just one vantage point. We monitored species, individuals, group formations, and broods. Brood sizes and duckling ages were classified according to Pirkola and Högmander (1974). Data concerning brood sizes and duckling ages were used to estimate brood numbers for each species in the given breeding season. We gathered enough data to perform detailed analyses of three out of the seven duck species observed: teal, mallard, and goldeneye.

For the analyses, we used the number of breeding pairs in May, following the Nordic methodology. Single males and pairs were assigned as breeding pairs (Koskimies and Väisänen 1991), with the addition that single females were also counted as breeding pairs according to the known conditions in the study area. Duck productivity was expressed as the ratio of the number of breeding pairs to the number of broods/ducklings per season. In this productivity calculation, we ensured that each brood was counted only once. To avoid pseudoreplication, we used brood size and age class information of the ducklings (see Nummi and Pöysä 1995b). A brood remains in each age class for ca. 1 week. Thus, in the second survey, we could back-calculate the age of each

Table 1 Study wetlands

Wetland	Shoreline (km)	Size (ha)	Coordinates (lat, lon)
Orastinsuo, Länsiallas	2.135	20.91	65° 17.606″ N, 26° 02.521″ E
Orastinsuo, Väliallas	0.987	5.42	65° 17.303″ N, 26° 03.142″ E
Orastinsuo, Itäallas	0.812	2.74	65° 17.076″ N, 26° 03.427″ E
Kamulanpuro	1.292	4.06	63° 46.269″ N, 25° 30.410″ E
Rypyharju	1.23	1.27	65° 23.522″ N, 26° 07.606″ E
Kattilapuro	0.927	3.83	63° 13.338″ N, 30° 30.049″ E
Lippi	0.863	1.86	63° 08.500″ N, 30° 32.907″ E
Saarikko	0.655	1.41	67° 92.671″ N, 33° 99.638″ E
Haarajärvi	0.645	1.87	67° 92.338″ N, 34° 02.918″ E
KirstinkorpiN	0.618	0.98	61° 53.843″ N, 23° 14.133″ E
KirstinkorpiS	0.458	0.63	61° 53.706″ N, 23° 13.996″ E
Varispuro	0.436	0.51	63° 13.738″ N, 30° 31.222″ E
Paloharju	0.292	0.46	65° 22.617″ N, 26° 06.376″ E

Fig. 1 Map of the study wetlands in Finland



brood during the earlier survey and evaluate whether we had seen the brood before; the number of ducklings could be used as a further means for brood identification. Moreover, the number of broods for each species per season normally ranged between zero and three (with the exception of two cases that had four and five broods, respectively) in one study wetland, which further eased brood identification. This method has been used in several studies during recent years (e.g., Nummi and Hahtola 2008; Väänänen et al. 2012; Nummi et al. 2019b). We also used the number of broods/ducklings per survey from June to August to track site preferences and use. We included the number of fledged ducks during the post-breeding phase in August because these data are important for hunting purposes. The densities are expressed as numbers per shoreline km, as has been done in most boreal duck research (e.g., Elmberg et al. 1993; Nummi and Pöysä 1993, 1995a, b); this also enabled comparisons with earlier studies.

Food resources

Aquatic invertebrates were sampled using 1-l glass jars with funnels (activity trap) attached to the edge of the jar (Elmberg et al. 1992). Samples were collected in June or the first half of July, depending on the phenology of each site, with the aim of targeting the same phase of invertebrate development at each site. Ten traps were placed on the shoreline of each wetland for 2 days, with the funnels directed towards the shoreline and completely submerged at a depth of 20–40 cm. After retrieving the traps, the captured invertebrates were assigned into species groups and classified into five size classes (0–1.3; 1.4–5; 5.1–10; 10.1–16.3; 16.4–30 mm) according to Nudds and Bowlby (1984), with small modifications according to Elmberg et al. (1993). Invertebrate biomass index was expressed per trap. Food abundance for each lake was indexed using the mean number of invertebrates per trap multiplied by their respective length (see more details in Nummi and Pöysä 1993).

Vegetation sampling

Vegetation development was measured using two line samples on each wetland. The vegetation line was 25 m long and originated on the shore, leading straight towards the center of the wetland. For each 0.5-m interval, all emergent plants found touching the line were recorded, along with the number of species (Danell and Sjöberg 1982). In cases where the water level was too low, the vegetation line was shortened according to each given situation. For the analyses, we used vegetation cover and the sum of the vegetation species detected in both lines for each wetland.

Statistical analysis

We performed all our statistical analyses using statistics software R (R Core Team 2019). We applied generalized linear mixed models (GLMM) with the package “glmmTMB” (Brooks et al. 2017) to analyze the effects of food availability and vegetation coverage on the duck pairs in spring, the duck broods in summer, and fledged duck densities in July–August. We included the lakes as random effects in the models because the observations were nested in the lakes naturally. As duck species richness follows a Poisson distribution, we applied Poisson GLMM to analyze how it was affected by food availability and vegetation. Duck density consists of zeros and positive

Table 2 Three common duck species (teal, mallard, goldeneye) on man-made wetlands in Finland during 2008–2011. Mean densities of pooled wetlands ($\bar{x}$) for pairs, broods, and fledged ducks in July–August (per km of shoreline), the number of broods per pair, the number of young per pair (breeding success × brood size at age class III); *SD* standard deviation, *R* yearly range of pooled data; numbers in parentheses represent total observations of pairs, broods, and fledged ducks in July–August

	Pairs/km shoreline	Broods/km shoreline	Broods/pair	Number of young/pair	Fledged ducks July–August/km shoreline
Teal					
$\bar{x}$	1.79	1.69	0.94	3.73	5.04
SD	2.04	1.37			7.08
R	1.67–2.98	1.05–1.93			4.40–6.48
	(103)	(60)			(682)
Mallard					
$\bar{x}$	0.82	0.15	0.18	1.15	1.53
SD	1.26	0.40			3.48
R	0.44–1.29	0.13–0.26			0.41–5.22
	(49)	(8)			(171)
Goldeneye					
$\bar{x}$	1.27	1.45	1.14	3.96	0.63
SD	1.53	1.66			1.60
R	0.26–2.08	0.79–1.50			0.15–2.27
	(71)	(48)			(68)

continuous values; thus, we applied GLMM with binomial distribution to analyze the presence and absence of the duck pairs and broods and GLMM with gamma distribution to examine the positive values of the duck pair densities and brood densities. Furthermore, we analyzed three species, i.e., mallard, teal, and goldeneye, for management purposes. We then examined the pair densities of the three species in spring, the brood densities of teals and goldeneyes in summer, and the fledged duck density of teals in July–August.

Results

A total of seven duck species were observed in the study wetlands. Teal, mallard, and goldeneye were found in study wetlands all over Finland, and they were also observed with broods. Interestingly, the endangered tufted duck (*Aythya fuligula*) and northern pintail, along with the rare smew (*Mergellus albellus*), were observed on the northernmost study wetlands, which may reflect their distribution in Finland (Appendix, Table 9). During the study period, teal pairs were observed on 12 wetlands, and their densities varied from 0 to 3.63 pairs per km/shoreline; mallard pairs were present on 11 wetlands, with densities ranging from 0 to 3.05 pairs per km/shoreline, and goldeneye pairs were observed on 10 wetlands, and their densities varied from 0 to 3.63 pairs per km/shoreline. Pairs of wigeon, tufted duck, and smew were present only on a single wetland each. Wigeon pair densities varied from 0 to 0.57 pairs per km/shoreline, tufted duck pair densities ranged from 0 to 1.41 pairs per km/shoreline, and smew pair densities varied from 0 to 0.19 pairs per km/shoreline.

Teal broods were present on all 13 wetlands, and their densities varied from 0.27 to 3.64 broods per km/shoreline, while mallard broods were present on five wetlands, and their densities ranged from 0 to 0.47 broods per km/shoreline. Goldeneye broods were present on 11 wetlands, and their densities varied from 0 to 4.96 broods per km/shoreline. Pintail broods were present on one wetland, and their densities varied from 0 to 0.40 broods per km/shoreline.

Fledged teal individuals were observed on 12 wetlands, and their densities varied from 0 to 20.73 individuals per km/shoreline. Fledged mallard individuals were observed on eight wetlands, and their densities ranged from 0 to 6.25 individuals per km/shoreline, while fledged goldeneye individuals were observed on nine wetlands, and their densities varied from 0 to 2.62 individuals per km/shoreline. Fledged individuals of wigeon and tufted duck were present on only one wetland each. Densities of fledged wigeon individuals varied from 0 to 0.12 individuals per km/shoreline, and densities of fledged tufted duck individuals varied from 0 to 2.43 individuals per km/shoreline (Appendix, Table 9).

For our pooled study wetland data, the average pair densities of the three common duck species (teal, mallard, goldeneye) varied from 0.82 to 1.79 pairs per km/shoreline (see Appendix, Table 9 for the density ranges of the individual wetlands during the study years: 0–3.63 pairs per km/shoreline), the average brood density of the investigated duck species varied from 0.15 to 1.69 broods per km/shoreline (0–4.96 broods per km/shoreline for individual wetlands during the study years), and the average density of the fledged ducks varied from 0.63 to 5.04 individuals per km/shoreline (0 to 20.73 individuals per km/shoreline for individual wetlands during the study years) (Table 2). The average invertebrate biomass index for the pooled 13

Table 3 The effect of food availability and vegetation cover on duck pair occurrence in man-made wetlands. The random effects of lakes σ_{lake} are 0.94^2

	Estimate	SE	*z*-value	*p*-value
Intercept	6.20	2.96	**2.09**	**0.036**
Invertebrate biomass Index	9.10	4.47	**2.03**	**0.041**
Vegetation cover	– 1.06	0.80	– 1.31	0.187

"*SE*" indicates standard errors. The same abbreviation is used in the tables below

Table 5 The effect of food availability and vegetation cover on duck brood occurrence in man-made wetlands. The random effects of lakes σ_{lake} is 1.02^2

	Estimate	SE	*z*-value	*p*-value
Intercept	0.65	0.36	1.78	0.075
Biomass index	0.06	0.21	0.31	0.75
Vegetation cover	0.10	0.34	0.29	0.76

"*SE*" indicates standard errors. The same abbreviation is used in the tables below

wetlands was 237.6 per trap (61.6–554.1 per trap for individual wetlands during the study years) (Appendix, Table 9).

Pairs in spring (May)

Our occurrence model showed that the invertebrate biomass index had a significantly positive effect on the presence of duck pairs (*p*-value = 0.041), while vegetation cover did not (Table 3). The conditional models showed that neither the invertebrate biomass index nor vegetation cover affected duck pair densities or species richness (Table 4). Neither covariate could explain the presence of mallard and teal pairs or their pair densities (Appendix, Table 10). The presence of goldeneye pairs, however, had a non-significantly positive correlation with the invertebrate biomass index (estimated parameter = 0.72, *p*-value = 0.089, Appendix, Table 10).

Duck broods during the brood-rearing period (June–August)

In the occurrence model, neither invertebrate biomass index nor vegetation cover (Table 5) could explain the presence or absence of duck broods. In the conditional model, the brood density, i.e., the number of broods per shoreline km, had a significantly positive correlation with the invertebrate biomass index (*p*-value = 0.002, Table 6) and a non-significantly negative correlation with vegetation cover. However, neither invertebrate biomass index nor vegetation cover could explain the species richness of duck broods (Table 6). No covariates can explain the presence or absence of our two target species broods, i.e., teal and goldeneye. Teal duckling densities correlated positively with the biomass index (*p*-value = 0.042) but not with vegetation cover (Appendix, Table 11). Our optimal model showed that goldeneye brood density tended to correlate positively with the biomass index (p-value = 0.081), while the effect of vegetation cover on goldeneye brood density was minimal (estimated parameter = – 0.09, *p*-value = 0.384, Appendix, Table 11). The effects of invertebrate biomass index and vegetation cover on mallard broods were not tested due to insufficient data.

Duck density during the post-breeding period (August)

Our models showed that neither food availability nor vegetation cover could explain the species richness of fledged ducks during the post-breeding period or their presence (Tables 7 and 8). However, duck density during the post-breeding period correlated positively with the invertebrate biomass index (*p*-value = 0.007) but not with vegetation cover (Table 8). Generally, the presence of fledged teals in July–August was not affected by food availability or vegetation coverage (Appendix, Table 12).

Discussion

To evaluate our hypothesis that man-made wetlands exhibit high duck habitat use during the breeding season, we compared our results with a study conducted in similar boreal oligotrophic lake areas in southern (Evo) and eastern (Intsilä) Finland (see Fig. 2, Nummi and Pöysä 1997a). This comparison is conservative, as only mallard populations

Table 4 The effect of food availability and vegetation cover on duck pair density and species richness according to conditional models. The random effects of wetlands σ_{lake} are 0.94^2 in the pair density model and 0.51^2 in the species richness model, respectively

	Duck pair density				Species richness			
	Estimate	SE	*z*-value	*p*-value	Estimate	SE	*z*-value	*p*-value
Intercept	1.70	0.14	11.39	**< 0.001**	0.40	0.20	2.00	**0.045**
Invertebrate biomass index	– 0.13	0.09	– 1.44	0.148	0.09	0.11	0.77	0.437
Vegetation cover	– 0.04	0.12	– 0.34	0.727	– 0.001	0.18	– 0.01	0.992

Table 6 The effect of food availability and vegetation cover on duck brood densities and species richness according to conditional models. The random effects of lakes σ_{lake} is 0.44^2 in the duck brood density model

	Duck brood density				Species richness			
	Estimate	SE	*z*-value	*p*-value	Estimate	SE	*z*-value	*p*-value
Intercept	0.76	0.15	5.07	**< 0.001**	0.39	0.08	4.93	**< 0.001**
Biomass index	0.20	0.07	2.96	**0.002**	0.09	0.08	1.21	0.226
Vegetation cover	− 0.13	0.10	− 1.22	0.219	− 0.005	0.08	− 0.07	0.943

Table 7 The effect of food availability and vegetation cover on duck occurrence during the post-breeding period (August). The random effects of lakes σ_{lake} is 0.90^2

	Estimate	SE	*z*-value	*p*-value
Intercept	0.76	0.38	1.97	**0.048**
Biomass index	− 0.16	0.25	− 0.64	0.520
Vegetation cover	0.32	0.36	0.89	0.373

Table 8 The effect of food availability and vegetation cover on duck density and species richness during the post-breeding period (August) according to conditional models. The random effects of lakes σ_{lake} is 0.55^2 in the density model

	Duck density				Species richness			
	Estimate	SE	*z*-value	*p*-value	Estimate	SE	*z*-value	*p*-value
Intercept	2.26	0.21	10.74	**< 0.001**	1.07	0.07	15.11	**< 0.001**
Biomass index	0.44	0.16	2.65	**0.007**	0.09	0.08	1.17	0.242
Vegetation cover	− 0.17	0.17	− 0.99	0.319	− 0.06	0.07	− 0.85	0.394

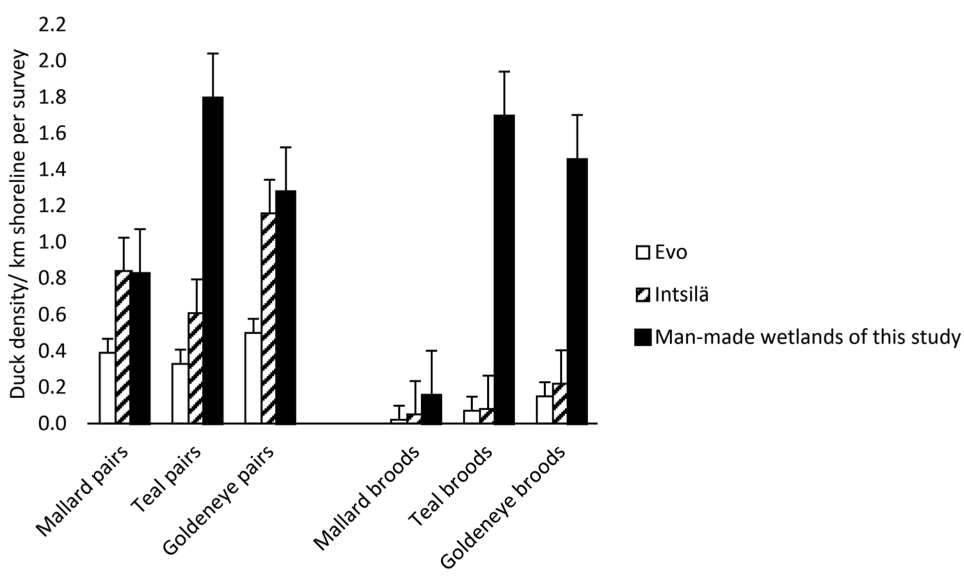


Fig. 2 A comparison of duck pair density and brood density (per km of shoreline) of the three common duck species (mallard, teal, and goldeneye) in our study wetlands (13 wetlands) across Finland during 2008–2011 and in two boreal areas; Evo in southern Finland (51 wetlands) and Intsilä in eastern Finland (23 wetlands) (Nummi and Pöysä 1997a). The bars represent standard errors

and their breeding success have remained similar during the time period between the data collection of these two studies, while the populations and breeding success of teal and goldeneye have decreased in Finland (Holopainen et al. 2018; LUKE 2021). During the comparison period of ca. 10 years, no effect has been found on teal and mallard breeding success (Arzel et al. 2014; see also Guillemain et al. 2013). Our results suggest that man-made wetlands are used by breeding ducks and are more productive than oligotrophic boreal wetlands in general in Finland, a pattern also found in beaver ponds (Nummi and Holopainen 2014). Pair densities of teal and goldeneye and brood densities of all the investigated species were higher in our study wetlands. The pair and brood densities of teal, which respond rapidly to flooding, were several times higher compared with the boreal lakes at Evo and Intsilä. Teals are known to rapidly occupy newly flooded beaver ponds: clearly higher teal pair and brood densities were detected in beaver ponds compared with non-beaver ponds in southern Finland (Nummi and Pöysä 1997b; Nummi and Hahtola 2008). This similarity between the occupancy in our study wetlands and beaver ponds can be interpreted as an *r*-selected strategy of the teal, which often rapidly inhabits newly created habitats (Nummi et al. 2015). Teal broods also more likely prefer bogs, fens, and small waterbodies in general (< 10 ha) (Decarie et al. 1995; Nummi and Pöysä 1995b), which correspond to man-made wetlands in characteristics and size.

This implies that numerous small and medium-sized wetlands are preferable to fewer large ones when designing wetlands with duck broods in mind (Walker et al. 2013). Furthermore, we found that the study wetlands had much higher duck productivity expressed by brood density and the number of young per pair than the boreal lakes at Evo (Nummi and Pöysä 1997a). The number of goldeneye broods per pair was over one, which means that these food-rich study wetlands attract broods from neighboring nesting sites. Regarding spatial ecology, man-made wetlands may be seen as hot spots for abundant food resources (Pickett and Rogers 1997). They act similarly to beaver ponds in a mosaic landscape of patches that increased teal brood densities at the patch level (Nummi et al. 2019b): also, the brood and pair densities of all three investigated species increased in the study wetlands. Even if the number of breeding ducks remains the same at the landscape scale, the habitat selection of brood-rearing female ducks may influence population-level breeding success. This is due to the potential impact on duckling survival rates, as optimal habitats provide shelter and food for ducklings (Simpson et al. 2007; Bloom et al. 2013; Holopainen et al. 2014a), subsequently influencing their survival (Gunnarsson et al. 2004; Nummi & Hahtola 2008).

Our results suggest that food availability is the determining factor influencing duck use in our study wetlands. The invertebrate indices of the man-made wetlands (Appendix, Table 9) were clearly higher than those in boreal ponds in general, and they resembled those found in beaver flowages in a similar boreal landscape (Nummi and Hahtola 2008). We found significant positive associations between the invertebrate biomass index and duck pairs, brood densities, teal duckling densities, and duck densities during the post-breeding period. We also found non-significant positive associations between goldeneye pairs, goldeneye duckling density, and teal duck density during July–August. Several studies from boreal wetlands show that invertebrate abundance is the key factor affecting the habitat use of breeding ducks (e.g., Nummi and Pöysä 1995b; Nummi et al. 2012; Holopainen et al. 2014a, 2015), and the same pattern seems to apply to man-made wetlands. However, not only is invertebrate biomass important but so also is their diversity in the boreal landscape, as food preferences vary between duck species (Nummi et al. 2013). This divergence, however, appears to diminish in habitats with very abundant food resources, leading to a higher diet overlap in these wetlands (Nummi and Väänänen 2001). Duckling diet varies not only among species but also depends on hatching date and lake circumstances (Bendell and McNicol 1995). Furthermore, we observed a negative effect of the invertebrate biomass index on duck pair density but without statistical significance. This may be explained by the different distributions of ducks during individual breeding phases, when breeding pair densities can be influenced by territoriality to where pairs do not have to occur concurrently in the most convenient luxuriant habitats (Nummi and Pöysä 1995b). Pairs are more mobile than broods so they can forage on surrounding lakes richer in food supplies. They also have more foraging opportunities on temporary wetlands in spring, e.g., on flooded shores and vernal pools (Nummi et al. 2019b).

We only found a weak effect of vegetation on duck habitat use; duck pairs, brood densities, and goldeneye ducklings were non-significantly negatively associated with vegetation cover. Previous studies from boreal wetlands in Finland and elsewhere show that vegetation is usually more important for dabbling ducks than diving ducks (Nummi and Pöysä 1993; Holopainen et al. 2015). This is especially true for mallard ducklings that search for food within the vegetated shoreline (Monda and Ratti 1988; Nummi et al. 2013) unlike goldeneye ducklings, which more frequently feed on nektonic prey in open water (Eriksson 1979). However, our results indicate that food availability is a more important factor than habitat structure for breeding ducks in man-made wetlands.

We observed that invertebrate colonization was rapid and was reflected by duck brood densities. The highest invertebrate abundance and species richness were found during the second year after flooding, which is in accordance with a study from Doñana, Spain, where invertebrate richness and diversity rapidly increased during the second hydroperiod of newly created ponds (Coccia et al. 2016). It gradually decreased in the study wetlands, which may have been caused by the decrease in particulate organic matter that is positively related to macroinvertebrate biomass (Danell and Sjöberg 1979; Stewart and Downing 2008). The change in invertebrate abundance and species composition in a man-made wetland in northern Sweden was also observed between the third and eighth years. Chironomids and *Asellus*, which are important duck food, decreased over time, and this trend was followed by decreased duck production (Danell and Sjöberg 1982). The colonization of newly created wetlands is usually very rapid, especially by well-dispersing invertebrates such as chironomids and dytiscids (Sjöberg and Danell 1983; Nummi et al. 2021). These were recorded between the first and third years on man-made ponds in Spain (Ruhí et al. 2009) and in a newly created pond in Switzerland, where chironomid abundance was comparable with older ponds during the first 3 years (Lods-Crozet and Castella 2009). Species compositions did not change significantly in either study. The similar pattern of high invertebrate development may also be seen in wetlands created by beaver flooding, where Cladocera had high densities in the first year after flooding, and chironomid and *Asellus* numbers were high from the second year onwards (Nummi 1989). Cladocera forms an important part of the teal diet (Nummi 1993). These findings imply that the early stages of succession are very productive regarding high invertebrate densities and consequently the presence of duck broods.

Boreal duck breeding habitats can be categorized at a large scale as either oligotrophic nutrient-poor lakes or eutrophic nutrient-rich lakes (Lehikoinen et al. 2016); the abundances of breeding pairs, broods, and juveniles usually increase with habitat luxuriance (Nummi and Pöysä 1993). In our study, man-made wetlands fit the eutrophic category, with high nutrient levels and food supplies, which may be due to the wetlands being created with dams; i.e., they receive nutrients from decomposing plants, and also because they are originally fishless. Fish, such as perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*), compete with ducks in boreal lakes for invertebrate resources, which negatively affects duck breeding success. This is especially true for the goldeneye because the species forages in open water (Eriksson 1983; Nummi et al. 2016). The abundance of fish species that are considered food competitors of ducks is a crucial factor influencing duck lake use in Finland—with a larger role than the presence of predatory fish such as pike (*Esox lucius*) (Väänänen et al. 2012). Even though our man-made wetlands were not stocked with fish, some small pikes were found in the invertebrate traps of certain lakes in 2010 and 2011. Fieldwork was conducted 3 years after the wetlands were established, so fish populations were probably not fully developed and did not significantly affect invertebrate levels. However, food competition between ducks and fish may intensify later.

Our findings can be used as a management tool for creating man-made wetlands targeted to increase duck productivity and diversity (Nummi and Holopainen 2020). Based on our results, the high abundance and diversity of aquatic invertebrates providing a rich food resource for ducks was the most important feature of these wetlands. Early successional stages may, in this regard, be very profitable, as the water contains a great deal of organic matter that increases invertebrate biomass and consequently increases duck brood densities. This should be considered when aiming to uphold high invertebrate abundances in the long term. This can be achieved by creating shallow wetlands with flooded shorelines or by altering the water levels of man-made wetlands every few years to improve waterbird food supplies (Whitman 1974; Lods-Crozet and Castella 2009). Although macrophyte vegetation was not an important factor in the study wetlands, it can also be considered, as it provides shelter and food for invertebrates and ducks (e.g., Nummi and Pöysä 1993). Optimal man-made wetlands for ducks should have areas with lush vegetation for dabbling ducks but also open water that is preferred, e.g., by goldeneyes. Ideally, they should also be fishless. Indeed, man-made wetlands are high-quality breeding patches for waterbirds in the boreal zone and may additionally be one solution for compensating wetland loss.

Appendix

Table 9 Summary data for each of the 13 man-made wetlands in Finland during 2008–2011. The table shows mean densities of pairs, broods, and fledged ducks in July–August (numbers per km of shoreline per survey) and the mean invertebrate biomass index per trap for the studied years

Wetlands	Species	Pairs/km shoreline	Broods/km shoreline	Fledged ducks in July–August/km shoreline	Invertebrate biomass index
Orastinsuo, Länsiallas					388.3
	Anas crecca	1.30	0.94	11.36	
	Anas platyrhynchos	1.17	0.47	6.25	
	Bucephala clangula	0.91	0.59	2.62	
	Mareca penelope	0.00	0.00	0.12	
	Aythya fuligula	1.41	0.00	2.43	
Orastinsuo, Väliallas					246.9
	Anas crecca	0.91	1.01	1.86	
	Anas platyrhynchos	0.00	0.00	0.51	
	Bucephala clangula	0.68	0.76	0.17	
Orastinsuo, Itäallas					156.0
	Anas crecca	1.23	0.62	2.21	
	Anas platyrhynchos	0.00	0.00	3.03	
	Bucephala clangula	1.64	1.85	0.00	
Kamulanpuro					198.4
	Anas crecca	2.90	1.55	3.42	
	Anas platyrhynchos	0.19	0.19	0.64	
	Bucephala clangula	1.06	0.58	0.13	
	Mergellus albellus	0.19	0.00	0.00	
Rypyharju					61.6
	Anas crecca	1.42	0.27	0.20	
Kattilapuro					261.2
	Anas crecca	1.80	2.52	3.42	
	Anas platyrhynchos	0.54	0.36	0.09	
	Bucephala clangula	1.08	0.72	0.09	
Lippi					148.3
	Anas crecca	0.29	1.16	0.14	
	Anas platyrhynchos	0.00	0.00	0.29	
	Bucephala clangula	0.00	0.58	0.00	
Saarikko					255.7
	Anas crecca	3.63	2.29	3.24	
	Anas platyrhynchos	3.05	0.38	3.94	
	Bucephala clangula	3.63	4.96	1.43	
	Mareca penelope	0.57	0.00	0.00	
Haarajärvi					132.0
	Anas crecca	1.55	1.94	0.19	
	Anas platyrhynchos	0.52	0.00	0.00	
	Bucephala clangula	1.55	1.16	0.10	
KirstinkorpiN					298.0
	Anas crecca	3.03	3.64	20.73	
	Anas platyrhynchos	1.62	0.40	2.02	
	Bucephala clangula	0.81	2.02	1.62	
KirstinkorpiS					554.4
	Anas crecca	1.91	2.18	6.55	
	Anas platyrhynchos	1.36	0.00	0.00	
	Bucephala clangula	0.82	1.64	0.45	
	Anas acuta	0.00	0.40	0.00	

Table 9 (continued)

Wetlands	Species	Pairs/km shoreline	Broods/km shoreline	Fledged ducks in July–August/km shoreline	Invertebrate biomass index
Varispuro					266.0
	Anas crecca	2.29	2.29	3.70	
	Anas platyrhynchos	0.38	0.00	0.00	
	Bucephala clangula	2.68	3.06	0.25	
Paloharju					122.4
	Anas crecca	0.00	1.14	0.00	

Table 10 ZAP model results for three duck species. The random effects of lakes are 1.11^2 for mallard, 0.97^2 for teal, and 1.17^2 goldeneye occurrence models, respectively

Mallard	Estimate	SE	*z*-value	*p*-value
Mallard				
Intercept	−0.86	0.50	−1.69	0.090
Biomass index	0.15	0.34	0.44	0.65
Vegetation cover	0.11	0.45	0.25	0.79
Teal				
Intercept	0.43	0.43	1.00	0.317
Biomass index	−0.01	0.32	−0.03	0.970
Vegetation cover	0.16	0.44	0.37	0.706
Goldeneye				
Intercept	0.36	0.49	0.74	0.454
Biomass index	0.72	0.42	1.69	0.089
Vegetation cover	−0.33	0.47	−0.70	0.483

Table 11 ZAP model results for teal and goldeneye broods. The random effects of lakes are 0.63^2 in the occurrence model for goldeneye and 0.30^2 in the conditional model, respectively. ZAP model results for teal and goldeneye. The random effects of lakes are 1.20^2 in the occurrence model and 0.51^2 in the conditional model, respectively

Teal	Occurrence model				Conditional model			
	Estimate	**SE**	***z*-value**	***p*-value**	**Estimate**	**SE**	***z*-value**	***p*-value**
Intercept	−0.22	0.26	−0.84	0.399	1.91	0.15	12.29	**< 0.001**
Biomass index	0.20	0.19	1.07	0.282	0.21	0.10	2.03	**0.042**
Vegetation cover	0.23	0.25	0.93	0.350	0.11	0.14	0.82	0.409
Goldeneye	**Occurrence model**				**Conditional model**			
	Estimate	**SE**	***z*-value**	***p*-value**	**Estimate**	**SE**	***z*-value**	***p*-value**
Intercept	−0.33	0.41	−0.80	0.422	0.36	0.16	2.20	**0.027**
Biomass index	0.22	0.25	0.86	0.386	0.15	0.08	1.74	0.081
Vegetation cover	−0.35	0.36	−0.96	0.333	−0.09	0.11	−0.87	0.384

Table 12 ZAP model results for teal density during the post-breeding period (August). The random effects of lakes are 0.68^2 in the occurrence model and 0.64^2 in the conditional model, respectively

Teal	Occurrence model				Conditional model			
	Estimate	**SE**	***z*-value**	***p*-value**	**Estimate**	**SE**	***z*-value**	***p*-value**
Intercept	0.11	0.30	0.36	0.713	1.91	0.26	7.26	**< 0.001**
Biomass index	0.07	0.23	0.30	0.758	0.28	0.21	1.32	0.186
Vegetation cover	0.38	0.30	1.25	0.211	0.01	0.20	0.09	0.926

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