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Source: Wildlife Biology, 2021(3)

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.00846

Wildlife Biology 2021: wlb.00846
doi: 10.2981/wlb.00846

Subject Editor: Matthieu Guillemain. Editor-in-Chief: Ilse Storch. Accepted 15 June 2021

Effects of released farmed mallards on species richness of breeding waterbirds and amphibians in natural, restored and constructed wetlands

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Common practices in current game management are wetland restoration and creation, as well as releases of quarry species. We studied the impact of releases of mallard ducklings on species richness of wild waterbirds and amphibians on three types of wetlands: natural, constructed and restored. Data on species richness, macrophyte cover and water characteristics (total phosphorous and pH) were collected at 32 sites in an agricultural landscape in southern Sweden. In total, 14 species of waterbirds were recorded, ranging from zero to seven per wetland and survey. Amphibians were present in 24 of the 32 wetlands; in total five species were found, ranging from zero to three per wetland. By using generalized linear modelling we found that wetland type best predicted waterbird species richness. Constructed wetlands had significantly more waterbird species, regardless of whether they were used for mallard releases or not. There were breeding amphibians in 62% of natural, 100% of restored and 77% of constructed wetlands. Breeding amphibians were present in 84% of wetlands without, and in 62% of wetlands with releases. However, included variables did not explain amphibian species richness in the wetlands. Releasing large numbers of mallards on a wetland and providing food ad libitum is likely to affect water quality, nutrient availability and predation pressure. Indeed, phosphorous levels were significantly higher in release wetlands, but no differences were found between wetland types. This means that mallard releases may increase nutrient loads in environments that are already eutrophied. However, in our study system releases did not influence species richness of waterbirds and amphibians locally. Constructing wetlands for mallard releases can thus have positive local effects on species richness.

Keywords: biodiversity, created wetlands, eutrophication, farmed, hand-reared, restocking, supplementary feeding, waterbirds, waterfowl

Due to an ever-increasing anthropogenic footprint we are witnessing a deepening biodiversity crisis. This predicament is evident at all spatial scales, from global to local (Hautier et al. 2009, Willis and Bhagwat 2009). Wetlands and their inhabitants are in an especially precarious situation, as draining and degradation have greatly reduced wetland numbers and quality, not least in temperate zone countries with intensive agriculture and forestry (Krug 1993, Čížková et al. 2013, Davidson 2014). As a countermeasure, restoration of degraded wetlands and creation of new artificial ones have become widespread in recent decades. Purposes range from flood reduction and nutrient retention, to preservation and restoration of biodiversity (Söderqvist 2002, Hansson et al. 2005, Zhang et al. 2020). The success of initiatives of the latter type depends on wetland characteristics, earlier studies showing that factors such as size, basin shape, depth and vegetation may strongly influence species richness (Hansson et al. 2005, Ma et al. 2010, Zhang et al. 2020). Hence, the construction design of new and restored wetlands is likely to affect the number of species subsequently associated with them. Shallow wetlands with plenty of macrophytes generally have higher diversity than steep-sloped wetlands with little vegetation (true for a range of animal taxa, cf. Hansson et al. 2005, Liao et al. 2020). However, it is widely argued that they do not substitute natural wetlands, as these often have additional species rarely found in man-made or restored wetlands (Brown and Smith 1998, Sebastián-González and Green 2016, Almeida et al. 2020).

One reason for restoring wetlands is to increase the number of game birds. In North America, widespread wetland restoration has been successful at increasing the annual hunting bag of waterfowl (Nichols et al. 1995). In Europe, too, wetland restoration occurs on a large scale, but the aims are primarily to create nutrient traps, promote flood control and restore biodiversity (Pfadenhauer and Grootjans 1999), rather than to increase hunting bags on a continental scale. Instead, wildlife managers often seek to increase the number of waterfowl available to hunters locally by releasing farmed birds and providing them with supplementary food (Champagnon et al. 2013, Söderquist et al. 2014). The success of releases of farmed birds varies considerably, and the practice may entail unforeseen long term consequences, such as genetic introgression and morphological changes (Söderquist et al. 2014, 2017). The impact of releases on co-occurring species through e.g. interspecific competition, predation, predator attraction, habitat alteration and introduction of disease is often unpredictable (Champagnon et al. 2012b, Mustin et al. 2018). For example, as releases of game birds are usually followed by predator control and supplementary feeding, local species composition may be affected through changes in predation pressure, competition and nutrient status of the wetland. In turn, this may alter species composition and diversity of target wetlands. Whether this is the case in waterbirds has not yet been investigated. In a review of effects of releases of galliform game birds, supplementary feeding and predator control, Mustin et al. (2018) found mixed results regarding the abundance and diversity of co-occurring species. Predator control had a positive impact on breeding success and abundance, whereas supplementary feeding and releases did not have any effects on other species.

In this study we focus on the effects of releases of mallards *Anas platyrhynchos* on species richness in recipient wetlands. The mallard is widely distributed and the world's most numerous duck (Young 2005). It is also an important quarry species with annual harvests estimated at 4.5 million each in Europe and North America (Hirschfeld and Heyd 2005, Raftovich et al. 2011). Mallards breed in a wide range of wetland types, many of which have historically been reduced in extent and quality (Gibbs 2000, Davidson 2014). It is also a popular species when it comes to releases to increase harvest possibilities.

In Europe alone, approximately three million mallard ducklings are released each year for hunting purposes (Champagnon et al. 2013). Numbers vary considerably among countries; in some the number of released birds exceeds the natural population, whereas in other countries the practice is only marginal compared to the number of wild origin birds. For example, in France, with an estimated breeding population of 30 000–60 000 pairs (BirdLife International 2004), 1.4 million mallards are released annually (Champagnon et al. 2013). In Sweden, with an estimated breeding population of about 200 000 pairs (Ottosson et al. 2012), more than 250 000 ducklings are released each year (Söderquist 2015), whereas some countries have banned releases altogether (e.g. Norway). On the continental scale these activities involve thousands of wetlands of different size and biodiversity. Arguably, mallard releases constitute one of the largest unintended ecological experiments in this part of the world. The effects of releases on mallard genetics, morphology and population ecology have attracted research interest recently (Champagnon et al. 2009, 2010, 2011, 2012a, b, 2016a, b, Söderquist et al. 2013, 2014, 2017), but the possible effects on co-occurring species remain more or less unknown.

Wetlands used for mallard releases range from natural sites with long temporal continuity, to previously degraded wetlands that have been restored, and recently constructed ponds without a wetland pre-history. Wetlands of these three types were compared in two recent Spanish studies, which found that constructed wetlands were characterized by lower biodiversity than restored and natural (Sebastián-González and Green 2016, Almeida et al. 2020). The generality of these findings is worth exploring, not least since releases of farmed mallards are frequently carried out on restored or constructed wetlands. The latter are often seen as welcome additions to landscapes where extensive development has led to a reduction in wetland habitats for a wide range of species. For example, pond-breeding amphibians have undergone dramatic declines in agricultural landscapes, in which restoration and construction of wetlands are now seen as important countermeasures (Knutson et al. 2004, Porej and Hetherington 2005, Rannap et al. 2020). Further, amphibians are good indicators of wetland status, as they are sensitive to acidification and eutrophication (Knutson et al. 2004, Porej and Hetherington 2005, Shulse et al. 2010). Presence of breeding amphibians can thus serve as an indicator of pond level biodiversity (Knutson et al. 2004, Rannap et al. 2020).

Released mallards are often very sedentary following release; i.e. during their first months they only rarely leave the wetland where they were introduced (Söderquist 2015). They are therefore unlikely to cause an influx of nutrients from surrounding areas, as wild waterbirds frequently do (Dessborn et al. 2016). Releases may, however, boost local nutrient levels in wetlands as a result of managers' supplementary feeding. Much of the grain will be consumed by the ducklings (and other waterbirds) and their faeces will end up in the water, leading to elevated nutrient levels. A high local density of waterbirds, as is usually the case when mallard ducklings are released, may also affect the habitat by stirring up sediments and reducing macrophyte cover through grazing and grubbing (Søndergaard et al. 1996, Sandsten 2002), often creating a turbid state wetland.

Other ways in which released mallards can affect species richness is through interspecific competition. Although supplementary feeding is likely to reduce competition for food among ducks, an abundance of ducklings may nevertheless deplete natural food sources such as invertebrates and seeds, and thus decrease habitat quality for other species with similar diet. The elevated density of young mallards may also attract predators, but it is unclear if this increases per capita predation mortality (Connell 2000). Either way, it may influence the breeding success or habitat choice of wild conspecifics (cf. Dessborn et al. 2011) as well as other co-occurring species.

The aim of this study was to investigate the potential impact of releases of farmed mallards on wetland species richness, and whether such effects differ between natural, restored and constructed wetlands. We focused on waterbirds and amphibians, and also considered nutrient status.

Based on previous research (Sebastián-González and Green 2016, Zhang et al. 2020) we predicted that species richness of waterbirds and amphibians would be lower in constructed wetlands compared to restored and natural. We also predicted that wetlands, of any type, subjected to release of mallards, would have lower species richness of waterbirds and amphibians than wetlands without releases.

Material and methods

Study area

This study was carried out in the province of Scania in southernmost Sweden, which is dominated by intensive agriculture. Wetland loss has been massive for centuries in this region, but restoration and construction efforts have reversed the trend during the last three decades. Due to a combination of limestone bedrock, fertile soils and long-lasting nutrient leakage from agricultural land, nearly all wetlands in the region are alkaline and eutrophic. Commercial duck-hunting involving release of farmed mallards is commonplace at the larger estates in Scania. The standard practice is to release hundreds of ducklings, two to three weeks old, onto a wetland (usually in June), after which they are provided grain ad libitum. Duck hunting season starts 20 August, but the peak harvest of released mallards is in the second half of September.

In the municipalities of Vellinge, Malmö, Staffanstorp, Trelleborg, Svedala, Skurup and Ystad (55°24′–55°33′N, 13°06′–13°42′E) we selected 32 wetlands to be as similar as possible with respect to area and depth (mean ± 1 SD: 0.86 ± 0.62 ha and 1.19 ± 0.6 m). All were located in open agricultural landscapes with cropland or grassland as dominating surrounding land type. A clear-water state characterized most of the 32 wetlands, and only a few were very turbid. Wetlands represented three types defined as follows: 1) natural wetlands have not been physically altered in the last 100 years, most being glacial depressions, 2) restored wetlands are of natural origin, have been degraded, but subsequently restored in the last 5–15 years and 3) constructed wetlands are man-made with no wetland pre-history, typically the results of excavation in the last 5–40 years.

Of the 32 wetlands, 13 had a recent history of releases of farmed mallard ducklings for hunting purposes for several years. Five of the 13 release wetlands were constructed, seven were natural and one was restored. Of the 19 wetlands without mallard releases, seven were constructed, seven were natural and five were restored (Supporting information).

Data collection

Waterbirds

A first survey of all wetlands took place 22–24 May 2018, a time of year when all breeding birds have arrived and formed pairs. A second survey took place two months later, 16–18 July, well after releases of mallard ducklings, and when wild pond-breeding waterbirds have broods. Weather conditions were fair during all surveys; winds never amounted to more than a gentle breeze, and there was no or only light rain.

On arrival at a wetland, a point count of all birds with wetland affinity was carried out (numbers, pairs, broods, seen or heard; Koskimies and Väisänen 1991 for methodology) (Supporting information). If released mallards were present, these were counted too (mean ± 1 SD: 207 ± 136.7, range: 20–500), but they were not included in the dependent variable in subsequent analyses. Any wild mallard brood was readily distinguished from released mallards, as wild broods are led by their hen and ducklings are usually of a different age (i.e. development stage, which is easy to gauge) compared to released ducklings.

Amphibians and other fauna

During the regular waterbird surveys to the wetlands, which coincided with the peak chorusing period of late-breeding amphibians, all observations of amphibians as well as fish were noted. To better capture the occurrence of breeding amphibians, all wetlands were also visited once at night between 5 and 26 May solely for this purpose by hired experts. The latter surveys included listening for chorusing amphibians, as well as walking the shore with a flashlight to observe any non-calling individuals in the water.

Vegetation

On the first survey of a wetland, we noted dominating plant taxa along the shoreline as well as wetland macrophyte cover (floating and emergent; all species pooled) in percentage intervals (0 = none, 1 = less than 5%, 2 = 5–50%, 3 = more than 50%) (Supporting information).

Water characteristics

A water sample was collected in the deeper part of all wetlands on the first survey. pH was measured on site, and water samples were secured and frozen within 12 h for later analysis of nutrients (total phosphorus (P_{tot})). In the laboratory, water samples were poured through GF/C filters, after which total phosphorus was assessed according to the Swedish standard method (SS-EN ISO 6878:2005). Unfortunately, water samples from two wetlands were lost before analysis of total phosphorus.

Statistics

The number of waterbird species at each survey of a wetland was the dependent variable analysed by generalized linear modelling (Zuur et al. 2009) using the lme4 (Pinheiro et al. 2013) library with glmer function in R ver. 4.0.3 (<www.r-project.org>). We assumed a Poisson distribution and included a canonical log-link function. The model included four explanatory variables, of which two were factorial: 1) wetland type (1 = natural, 2 = restored, 3 = constructed), and 2) mallard releases (0 = no, 1 = yes). Because all wetlands turned out to be alkaline (Supporting information and Results), and due to overparameterization in the modelling, pH was subsequently excluded from the analysis. We subsequently omitted macrophyte cover and turbidity due to lack of variation. The only continuous explanatory variables were total phosphorus (P_{tot}) and wetland size (Supporting information), the data for which were normalized prior to modelling. Wetland ID was used as a random factor. However, as the random effect variance was found to be 0, it was omitted and we instead used generalized linear modelling with a glm-function from the package MASS (Venables and Ripley 2002) for the analyses. The model explaining waterbird species richness is as follows:

$$\text{Species number}_{ij} = \alpha + \beta \times X_i + \varepsilon_i$$

where Species number$_{ij}$ is the number of species in wetland i (1–32) and in survey j (first or second survey), α the model intercept, β the coefficient of the explanatory variable(s) X of wetland i, and ε_i a term representing unexplained noise. We also tried to fit interaction terms for wetland type and releases, but as it did not improve the model fit, we eventually used the main terms only. We also tested the possible effect of wetland age for the subset data including constructed and restored wetlands only. As it did not affect bird species richness, this variable was omitted from further analysis.

We explored all possible variable combinations by using only main effects including the intercept only model (in total 16 models) and ranked the candidate models by the Akaike information criterion with a correction for small sample sizes (AICc) to evaluate their relative fit with data (Burnham and Anderson 2002). Based on Akaike weights, we only present models within the 95% confidence set (i.e. the models with cumulative weights up to 0.95). We used model averaging for the 95% confidence model set and calculated the model-averaged parameters (β-values) and their standard errors and Z-values.

We used the same explanatory variables and modelling approach as above to study whether mallard releases affected amphibian species richness, based on pooled amphibian observations from the regular waterbird surveys and the dedicated amphibian surveys. In total, 16 models were considered.

To test if there was any difference in waterbird species richness between the first and second survey, we used the Wilcoxon signed ranks test, whilst the Mann–Whitney test was used to assess if amphibian species richness differed between wetland types. Fisher's exact test was used to analyse differences in macrophyte cover between wetlands with and without mallard releases, as well as among wetland types. Differences in P_{tot} and pH between wetlands with and without mallard releases were evaluated by independent samples t-test, and among wetland types by a one-way ANOVA and the Kruskal–Wallis test, respectively. Statistical analyses contrasting surveys (first versus second) and wetland types were performed in IBM SPSS statistics ver. 26.

Results

Waterbirds

Fourteen species of duck, goose, swan, rail and grebe were observed at the study sites (Supporting information). The total number of observed bird species per wetland and survey ranged from 0 to 7 (mean ± 1 SD: 2.28 ± 1.60) and decreased significantly from the first survey (2.75 ± 1.57) to the second (1.81 ± 1.51) ($Z=2.763$, n = 32, p = 0.006) (Table 1). This general difference was mainly driven by birds in the natural wetlands ($Z=2.672$, n = 14, p = 0.008), since corresponding temporal contrasts for restored and constructed wetlands alone were not significant (restored: $Z=1.000$, n = 6, p = 0.317 and constructed: $Z=1.003$, n = 12, p = 0.316). The decrease from the first to the second survey was similar for wetlands with and without releases (Supporting information).

Table 1. Mean number (± 1 SD) of waterbird species in 32 wetlands in Scania, Sweden, presented by wetland type (constructed, natural, restored), census period (early versus late survey) and occurrence of release of mallard ducklings. See Methods for definitions of wetland type.

	Releases		No releases		Total	
Type	Early	Late	Early	Late	Early	Late
Constructed	2.20 ± 1.30	3.40 ± 1.95	4.43 ± 1.99	2.29 ± 1.50	3.50 ± 2.02	2.75 ± 1.71
Natural	2.86 ± 1.21	1.43 ± 1.27	1.86 ± 0.90	0.71 ± 0.49	2.36 ± 1.15	1.07 ± 1.00
Restored	3.00	1.00	2.0 ± 0.71	1.80 ± 1.30	2.17 ± 0.75	1.67 ± 1.21
Total	2.62 ± 1.19	2.15 ± 1.77	2.84 ± 1.80	1.58 ± 1.30	2.75 ± 1.57	1.81 ± 1.51

When inspecting the models explaining bird species richness, the 95% confidence set included six models. All six showed equally good fit ($AIC_i - AIC_{min} < 2$), but the best fitting model included 'wetland type' and 'total phosphorus' (Table 2). Only wetland type explained species richness significantly, constructed wetlands having more species than natural and restored wetlands (Table 1, 3). There was some support for a positive effect of wetland size on species richness, but the model averaged result was not significant. Mallard releases showed no effect on waterbird species richness.

Amphibians and other fauna

Breeding amphibians were observed in 24 of the 32 wetlands (Supporting information). Most had only one or two species. Edible frog *Pelophylax kl. esculenta* was the most widespread taxon, recorded in 23 of the 24 wetlands hosting amphibians. Common toad *Bufo bufo* was recorded in four, common frog *Rana temporaria* in three, smooth newt *Lissotriton vulgaris* in two and European fire-bellied toad *Bombina bombina* in one wetland. The proportion of wetlands in each type that had at least one species of breeding amphibian was 64% (9 of 14) in natural, 100% (6 of 6) in restored and 75% (9 of 12) in constructed. Sixteen out of 19 (84%)

Table 2. The 95% confidence set of models explaining species richness of waterbirds in 32 wetlands in Scania, Sweden. The models are ranked by AICc-values.

Model	df	AICc[a]	ΔAICc[b]	w[c]	C-W[d]	E-ratio[e]
Type + P	4	212.2	0.00	0.23	0.23	1.00
Type + Size + P	5	212.4	0.15	0.21	0.44	1.08
Release + Size + P	4	213.3	1.02	0.14	0.57	1.67
Size + P	3	213.3	1.09	0.13	0.71	1.72
Type + Release + P + Size	6	213.4	1.18	0.13	0.83	1.80
Type + Release + P	5	213.7	1.47	0.11	0.94	2.08

Type = wetland type, Release = mallard releases, Size = wetland size, P = total phosphorus. [a] Akaike's information criterion with a correction for small sample sizes. [b] Difference between the current model and the minimum AICc-value. [c] Model weight. [d] Cumulative weight. [e] Evidence ratio (w_{best}/w_i).

Table 3. Model-averaged coefficients (conditional average) for the 95% confidence set of models explaining species richness of waterbirds in 32 wetlands in Scania, Sweden (models listed in Table 2). Type = wetland type (natural wetland category represented by the intercept), P = total phosphorus, Size = wetland size and Release = occurrence of mallard releases.

Model	Estimate	SE	*Z*-value	p-value
Intercept	0.46	0.21	2.152	0.031
Type: Restored	0.09	0.29	0.290	0.772
Type: Constructed	0.50	0.21	2.345	0.019
P	−0.24	0.61	0.384	0.701
Size	0.95	0.52	1.798	0.072
Release	0.24	0.19	1.200	0.230

Table 5. Model-averaged coefficients (conditional average) for the 95% confidence set of models explaining species richness of amphibians in 32 wetlands in Scania, Sweden (models listed in Table 4). Type = wetland type (natural wetland category represented by the intercept), P = total phosphorus, Size = wetland size and Release = occurrence of mallard releases.

Model	Estimate	SE	*Z*-value	p-value
Intercept	−0.04	0.31	0.121	0.904
Type: Restored	0.81	0.48	1.603	0.109
Type: Constructed	0.57	0.42	1.299	0.194
P	−0.44	1.19	0.351	0.725
Size	0.27	0.79	0.331	0.740
Release	−0.18	0.39	0.433	0.665

wetlands without mallard releases had at least one species of breeding amphibian, whereas this was the case in eight out of 13 (62%) of wetlands with mallard releases.

When species richness of amphibians was analysed, the 95% confidence set included ten models, indicating some uncertainty in the results. The model with the best fit included 'total phosphorus' only, but model averaging showed no significant effects (Table 4, 5).

Although our methodology did not include a proper fish survey, we visually recorded fish in 17 of the 32 wetlands (Supporting information). Out of the 24 wetlands with breeding amphibians, 13 also harboured fish. Out of the 17 wetlands with fish, 13 also had breeding amphibians.

Vegetation

Grasses (*Poaceae* spp.) comprised the dominating shoreline vegetation in 21 of the 32 wetlands. Nettles (*Urtica* spp.) and common reed *Phragmites australis* were the dominating shoreline taxa in nine wetlands each (Supporting information). Sedges (*Carex* spp.) dominated in four wetlands, and bulrush (*Typha* spp.) in three. Rush (*Juncaceae* spp.), alder *Alnus glutinosa*, Wych elm *Ulmus glabra* and Norway spruce *Picea abies* were dominating at two wetlands each. Butterbur (*Petasites* spp.), dandelions (*Taraxacum* spp.), willows (*Salix* spp.), yellow iris *Iris pseudacorus*, wild cherry *Prunus avium*, hawthorn (*Crataegus* spp.) and elder *Sambucus nigra* were among the dominating shoreline taxa at one wetland each

Table 4. The 95% confidence set of models explaining species richness of amphibians in 32 wetlands in Scania, Sweden. The models are ranked by AICc-values.

Model	df	AICc[a]	ΔAICc[b]	*w*[c]	C-W[d]	E-ratio[e]
P	3	81.6	0	0.35	0.354	1.00
Type + P	4	83.7	2.1	0.12	0.478	2.85
Release + P	4	83.9	2.25	0.12	0.593	3.08
Size + P	5	84.1	2.43	0.11	0.698	3.37
Null model	5	84.9	3.3	0.07	0.766	5.21
Type	5	86.2	4.52	0.04	0.803	9.57
Type + Size + P	6	86.5	4.87	0.03	0.834	11.42
Type + Releases + P	6	86.5	4.87	0.03	0.865	11.42
Releases + Size + P	2	86.5	4.88	0.03	0.896	11.42
Size	2	86.5	4.9	0.03	0.927	11.42

Type = wetland type, Release = mallard releases, Size = wetland size, P = total phosphorus. [a] Akaike's information criterion with a correction for small sample sizes. [b] Difference between the current model and the minimum AICc-value. [c] Model weight. [d] Cumulative weight. [e] Evidence ratio (w_{best}/w_i).

(Supporting information). As more than one taxon may be dominant at a wetland, the sum of dominating taxa exceeds the total number of wetlands.

When it comes to macrophyte cover, 68% of the non-release wetlands had a score in category 0–2 (i.e. ≤ 50% cover), which was not significanly different from the corresponding value (92%) for mallard release wetlands (Fisher's exact test: p = 0.195). Also, macrophyte cover did not differ significantly between wetland types (Fisher's exact test: p ≥ 0.365; categories 0–2 merged in both analyses due to low sample sizes; Supporting information).

Water characteristics

Total phosphorous levels was significantly higher in wetlands where mallards were released (mean ± 1 SD: 261 ± 426 µg l^{-1}) than in non-release wetlands (43 ± 36 µg l^{-1}) (Supporting information) (independent samples t-test of log-transformed values, and with unequal variances assumed: t = −2.485, df = 16.153, p = 0.024). In contrast, total phosphorous did not differ among wetland types, i.e. natural, restored and constructed (one-way ANOVA based on log-transformed values: $F_{2,26} = 1.541$, p = 0.233).

All pH values were in the alkaline spectrum, ranging from 7.24 to 9.83 (8.26 ± 0.60), and did not differ significantly between release and non-release wetlands (independent samples t-test: t = −0.420, df = 30, p = 0.677), nor among the three wetland types (Kruskal Wallis: $H = 4.540$, df = 2, p = 0.103) (Supporting information).

Discussion

Effects of releases

Waterbirds

Contrary to our prediction, release of mallards did not appear to affect waterbird species richness. There is, to the best of our knowledge, not any previous study explicitly contrasting otherwise similar wetlands with and without releases of mallards for hunting purposes. Given this lack of comparison, we are cautious to draw any conclusions about the processes behind the patterns found. On the one hand, despite the number of birds involved, releases carried out at our study sites may be genuinely neutral with respect to other waterbird species. Alternatively, it may be that negative effects (e.g. predator attraction, habitat alteration) and positive effects (e.g. heterospecific attraction, predator swamping, supplemental feeding) cancel each other out. Further experiments are needed to tease these possible scenarios and effects apart.

However, there is one detail in our data that might indicate a negative (intraspecific) effect on wild mallards; wetlands with releases went from 77% having wild mallards present in the first census to 23% in the second, i.e. after addition of farmed ducklings. In wetlands that were not subjected to releases, wild mallard presence decreased from 53% to 42% (absence–presence data in Supporting information). However, these temporal changes were not statistically different from each other (Fisher's exact test: $p=0.267$ and $p=0.45$ respectively). It has long been debated whether large numbers of birds can provide some kind of safety-in-numbers or if large flocks instead attract more predators, increasing per capita predation risk. As Connell (2000) suggested, this may depend on the type of predator in question. In our study system it is fair to assume that released ducklings will increase visitation rate of predators such as crows, large gulls and mink in or around the wetlands, but whether this actually affects survival of wild species is less certain.

As is evident from Supporting information, our study sites collectively harboured a wide variety of wetland birds. The 14 recorded species include swans, geese, shelduck, dabbling ducks, diving ducks, grebes and rails, in other words representatives from all functional groups of waterbirds breeding in the region. Moreover, our sample included wide-spread generalist species (e.g. mallard, tufted duck *Aythya fuligula*, and goldeneye *Bucephala clangula*) as well as stenotopic and regionally rare species (e.g. gadwall *Anas strepera*, little grebe *Tachybaptus ruficollis*, red-necked grebe *Podiceps grisegena* and moorhen *Gallinula chloropus*). This list of species can be seen as representative for similar wetlands of this size in the region (Ottosson et al. 2012). More importantly, our sample of wetlands was not biased towards species-poor environments or those hosting only a certain functional group of waterbirds. The general decrease in species number observed from the first to the second survey is natural, as some breeding attempts fail and some species become more seclusive and hard to spot when they have young.

Amphibians

We recorded five out of the seven amphibian species occurring in the study region. The two 'missing species' (crested newt *Triturus cristatus* and moor frog *Rana arvalis*) are widespread in southern Sweden and fairly generalist, why their absence from our sample is a sign of a generally depauperate amphibian fauna at the landscape level. This impression is reinforced by the fact that another eurytopic and widespread species, the smooth newt, occurred in only two of 32 wetlands. Unlike in waterbirds, there was thus a bias towards amphibian communities dominated by a few generalists. Although indicative of regional conditions, this may reduce the value of our study as a benchmark for the rest of Sweden, but less so for areas in central Europe dominated by agriculture.

Fewer wetlands (62%, Supporting information) with mallard releases had amphibian species present than wetlands without releases (84%). Yet, mallard releases did not affect species richness of amphibians according to our modelling analysis (Table 4). This is despite the fact that many amphibians – adults as well as larvae – are prey to several of the recorded bird species, including mallards (reviewed by Cook 1987, Günther 1996). In other words, adding many mallard ducklings is expected to reduce survival of amphibian larvae and metamorphs. Further, salamanders and ducks may have a dietary overlap when feeding on pond invertebrates and they can thus compete for food (Benoy et al. 2002). In conclusion, the model for amphibian species richness, too, yielded a result contrary to our prediction. Moreover, none of the variables included explained amphibian species richness, which is surprising and calls for inclusion of further variables, such as fish abundance, in future studies.

Effects of wetland type

The best predictor of waterbird species richness included wetland type, with constructed wetlands having the highest richness. Constructed wetlands are clearly important for a range of species and they can therefore increase the biological diversity in a landscape even when they are created for other purposes (Ghermandi et al. 2010). It is not clear why constructed wetlands in our study area were more species-rich than natural. We do not think it had to do with landscape configuration, i.e. a consistent difference among the wetland types in isolation or connectivity. A more possible explanation is that the physical disturbance when a wetland is created or restored may have favoured some species. Schummer et al. (2012) found that wetlands restored by dredging had greater diversity of invertebrates and plants than did natural ones, and they speculated this was because the disturbance created more varied habitats and also exposed seed banks. Similarly, new wetlands created by beavers (*Castor* spp.) attract many breeding waterbirds, likely a result of nutrient release and elevated invertebrate abundance (Nummi and Holopainen 2014), and also benefit amphibians (Vehkaoja and Nummi 2015). Another possible explanation is that younger wetlands may not yet have been colonized by fish, which have a negative impact on breeding waterbirds as they may compete for invertebrate prey and depredate on juvenile birds (Elmberg et al. 2010, Dessborn et al. 2011). The presence of amphibians in at least 24 out of 32 wetlands is also an indication that fish predation is relatively low in most (Shulse et al. 2010).

However, created and restored wetlands are not always more diverse than natural ones. Many studies show no to little difference between wetland types when it comes to species richness (Delphey and Dinsmore 1993, Brown and Smith 1998, Hopple and Craft 2013), often with slightly more species in natural wetlands. Other studies have shown that natural wetlands are more important for biodiversity because they hold more rare species (Sebastián-González and Green 2016, Reeder and Wulker 2017). Many rare species are slow colonizers and more prone to occur in stable habitats (Iversen et al. 2013). The underrepresentation of such species in created and restored wetlands may therefore diminish over time. This view concurs with studies showing that older constructed wetlands have species compositions resembling those of natural wetlands (VanRees-Siewert and Dinsmore 1996, Reeder and Wulker 2017). As constructed and restored wetlands age they become more similar to natural wetlands in terms of vegetation and shoreline structure, which would gradually lead to a more similar species composition (Brown and Smith 1998). As an example, Delphey and Dinsmore (1993) found that certain shoreline vegetation types were absent in the restored potholes they investigated, which likely had an influence on bird species composition.

Water characteristics

Because total phosphorous had no significant effect on waterbirds or amphibians, we did not find support for nutrient level having a strong impact. However, total phosphorous level turned out to differ significantly between wetlands where mallards were released and those without releases. As all study wetlands are in a region with intensive agriculture, generally elevated concentrations can be expected. Indeed, the total phosphorus concentrations in wetlands without releases can be regarded as high (25–50 $\mu g\ l^{-1}$) and wetlands with releases as extremely high (> 100 $\mu g\ l^{-1}$) (Wiederholm 1999). In contrast, phosphorous levels did not differ among wetland types, indicating that mallard releases lead to eutrophication. This is likely due to the fact that supplemental food, usually cereal grain, is added in large quantities at wetlands where mallards are released, i.e. roughly 50 g per mallard and day. This corresponds to about 0.2 g phosphorous per duck and day based on concentrations in barley (ca 4 g kg^{-1}) reported by Salo et al. (2014). Similar relationships between mallard releases and nutrient concentrations in recipients have been shown before (Noer et al. 2008), and may potentially have great impact on wetland dynamics since phosphorous is normally the most limiting nutrient (Correll 1998). Adding nutrients to a wetland can, at least initially, promote macrophyte growth, which can favour many waterbirds. However, as a wetland becomes more eutrophic the water often turns turbid, which reduces submerged macrophytes when not enough light any longer penetrates the water column. The number of consecutive years of supplemental feeding likely affects the state of the water, but unfortunately exact data about this were not available for the wetlands in this study. While eutrophic lakes are known to support more diverse waterbird communities in general terms (Pöysä et al. 2019), diving ducks and grebes may become less numerous in artificially eutrophied compared to naturally eutrophied wetlands (Nilsson 1978, but see Fernández et al. 2005). In fact, Lehikoinen et al. (2016) showed that populations of three out of five waterbird species in Finland had negative long-term trends in eutrophic wetlands, but not in oligotrophic. On the other hand, Pöysä et al. (2019) found a positive effect of habitat luxuriance (as a proxy of trophic status) on waterbird colonization rates, but argue that this is a short-time effect and that consequences of eutrophication are expected to be negative in the long run.

Invertebrate abundance is also important for waterbirds, particularly during the breeding season (Dessborn et al. 2009). Eutrophication can lead to increased density of invertebrates as productivity increases, however, if there are fish in the wetland the result is often the reverse, as turbid states favour small fish that efficiently prey on invertebrates (Harper 1992). Released ducklings may also create a turbid state by disturbing sediments, as they occur in unnaturally high densities. Eutrophication and reduced water quality have impacts on other fauna as well. Knutson et al. (2004) found a trend for reduced breeding success in amphibians in farmland ponds with elevated phosphorous levels in a Minnesota setting with many similarities to our study area.

Because we sampled phosphorous in late May, i.e. before the annual release of mallards, the elevated concentrations found by us are likely due to food addition in previous years (e.g. sediment leaking). The potential consequences of mallard release practices for nutrients, constituting the base in the aquatic food chain, may therefore prevail long after the actual release activity. Since mallard ducklings are normally released in large numbers on single wetlands, related eutrophication concerns and consequences to wetland ecosystems need more attention in future studies. This is warranted by the fact that a low number of species tend to dominate and make up much of the total biomass in highly eutrophic wetlands (Harper 1992).

Other factors and sources of error

Fish were observed in about half of the wetlands. However, no proper fish inventory (netting or electro-fishing) was carried out and fish presence is likely underestimated. This is also the reason why possible effects of fish presence were not evaluated in this study. It is noteworthy, though, that out of the 17 wetlands with confirmed fish presence, 13 also had breeding amphibians. Previous studies show that predatory fish negatively affect species richness of amphibians (Hecnar and M'Closkey 1997, Knutson et al. 2004) and birds (Elmberg et al. 2010).

Other shortcomings of this study were: 1) wetlands were surveyed for amphibians in May only. As a result, early breeding species such as common frog, moor frog and common toad may be underrepresented. Even if this were the case, though, it would not change our general conclusions about amphibians, as the early breeding species, too, are widespread eurytopic species; 2) unlike natural wetlands, restored wetlands were treated 5–15 years prior to our study, and constructed were created 5–40 years before it. Therefore, we acknowledge that restored and created wetlands in the far ends of their respective time interval may differ in successional stage, and hence also in species richness of birds and amphibians.

Conclusions

We found that releases of mallard ducklings did not have any impact on species richness of waterbirds or amphibians in our study area. Even though releases did affect nutrient status in the wetlands, this in turn, had no obvious effects on number of species. Wetland type explained most of the differences in species richness, that is, constructed wetlands had the highest number of species of waterbirds. This is good news for conservation and wildlife management as it means that new wetlands can be an important refuge for species whose natural habitat has been reduced during decades of drainage and other human alterations. Even when constructed wetlands are used for large scale releases of mallards, the positive impact on species richness remains. However, many constructed wetlands are created for nutrient retention rather than increasing wetland habitats. With this purpose, mallard releases are counterproductive as they cause elevated nutrient levels.

Acknowledgements – We are grateful to the landowners that agreed to take part in this study. We also would like to thank Bettina Ekdahl and Alexander Nordström for help with amphibian surveys. *Funding* – This study was funded by grant 16/83 NV-00695-17 from the Swedish Environmental Protection Agency to JE. A grant from the Osk. Huttunen foundation to SH is much appreciated.

Author contributions

Pär Söderquist, Johan Elmberg and Gunnar Gunnarsson did field work, analyses and wrote the manuscript. Lisa Dessborn was involved in analyses and writing the manuscript. Henric Djerf did field and laboratory work, as well as commented on the manuscript. Sari Holopainen performed statistical modelling and commented on the manuscript.

Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.f7m0cfxwh> (Söderquist et al. 2021).

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