



Restoration of wetlands in the agricultural landscape for birds: management and species interactions

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Abstract

Wetland birds have been declining worldwide due to the habitat loss caused by the farming activities. Therefore wetland restorations are practised worldwide in order to recover the habitat of wetland birds. Most restoration measures covered in the literature consist of the recovery of wetland connectivity, manipulation of size, depth, and shape, and an introduction of grazing or mowing. The restoration projects focus on the improvement of the water quality and its suitability for the diverse needs of wetland birds: grazing and flooding will affect the vegetation structure benefiting different breeding requirements, including food and nest site availability. Even though wetland restorations have been implemented in many countries, the success of restorations is not commonly evaluated. However, among the few studies evaluating the effects of restoration measures on biodiversity, the results are variable: positive effects on wader, duck, grebe and heron species, while others find no recovery of bird diversity. The lack of effects on wetland bird diversity can be due to the negative effects of intense grazing or flooding on the nesting success (cattle may destroy the nests by trampling, where flooding by drowning). But it can be also that there are other effects involved, as some wetlands still stay unoccupied or have low species diversity. One possibility is that restoration measures or landscape composition may have an effect on the species interactions, such as predator-prey, heterospecific and conspecific competition and attraction. Thus, a more detailed investigation of the effects of wetland restorations on the bird species occurrence and how species interactions are affected by different restoration measures will improve our efficiency in the restorations of wetlands in an agricultural landscape.

Introduction

Wetlands are crucial for human well-being as they provide many ecosystem services, such as sediment filtering, carbon storage, freshwater, food and material provision, biodiversity, protection from flooding, climate change mitigation, nutrient retention (Bregnballe et al., 2014; Zedler and Kercher, 2005). However, due to human activities, such as urbanisation, drainage due to farming and pollution, more than 50% of wetland habitats worldwide have been lost or degraded in quality (Zedler and Kercher, 2005; Smart et al., 2006). Luckily, many countries acknowledge the importance of wetlands, and around 160 countries are involved in wetland management and preservation through the Ramsar Convention, and many countries have implemented policies to restore the lost and degraded wetlands (Schleupner and Schneider, 2013). The evaluation of the effects of wetland restorations is normally done by monitoring some specific species, e.g. wetland birds, as they are known to respond fast to the habitat changes (reflected in the species richness and abundance) and are easy to count (Sebastián-González and Green, 2016). Furthermore, wetland birds are declining and therefore are in a need of conservation actions (Smart et al., 2006). Other values of wetland birds include aesthetic values and that bird watching, in general, is an attractive activity for humans (Green and Elmberg, 2014).

The question is, what do we know about the effects of wetland restoration on wetland bird species richness and abundance? Do all bird species benefit from certain measures in the same way? How many studies have actually evaluated the effect of wetland restorations on birds? Are the restorations for birds efficient in terms of increasing species richness and abundance, and do the restoration measures have effects on species interactions, such as between predators and prey?

Here I will review the restoration measures and management strategies that have been used for the wetland restorations with the aim to increase wetland bird diversity. In the last part, I will also cover some of the literature concerning species interactions as these may have strong effects on the bird community structure of restored farmland wetlands.

Measures used in wetland restoration and their ecological background

It has been noted that restored wetlands can potentially recover biological processes that natural wetlands have and therefore reach similar levels of species richness (Sebastián-González and Green, 2016). Large-scale programs have been implemented to restore the farmland wetlands in the United States of America (USA), Europe and Canada, and these schemes are based on collaborative work between the state and farmers (Breeuwer et al., 2009; O’Neal et al., 2008; Stevens et al., 2003). For example, in the USA, the Wetland restoration programme and Conservation Reserve Enhancement Program (CREP) are supporting local initiatives to provide local habitat for water birds and stopover sites for migrants (O’Neal et al., 2008). Similar initiatives exist in Europe – through agri-environmental schemes (AES), national environmental protection agencies and other, non-governmental, organizations.

Only a few papers have clearly described the measures that were taken in order to restore wetlands in the agricultural landscape and even fewer have evaluated the effects in terms of bird diversity. Different countries may have somewhat different restoration measures and strategies to increase the bird diversity, but the majority have similar measures. Restoration of marsh and wet meadow ecosystems includes restoration of natural or regulated flooding regimes and natural wetland hydrology, for example in the USA, Italy, China, Belgium, Spain and United Kingdom (Root-Bernstein and Frascaroli, 2016; O’Neal et al., 2008; Jiang et al., 2016; Gerard et al., 2008; Eglington et al., 2008; Clausen and Madsen, 2016; Sebastián-González and Green, 2016). The restoration of floodplains do not just only benefit biodiversity, it also reduces the risk of flooding the cities and arable fields downstream, as the floodplains can quickly retain high rising water and act as a buffer (Platteuw et al., 2010). Grazing or mowing is typically introduced in wet grassland restorations (Olsen and Schmidt, 2004; Voslamber and Vulink, 2010; Źmihorski et al., 2016). Furthermore, many countries increase the area of open water in wetlands that otherwise would be covered by reeds and grasses (Clausen and Madsen, 2016; Stevens et al., 2003; Eglington et al., 2008; O’Neal et al., 2008). The reduction in the intensity of agricultural activity (Clausen and Madsen, 2016), the increase of water depth by removing debris (Stevens et al., 2003), or constant filtering of nutrient content (Noordhuis et al., 2002; O’Neal et al., 2008) could be also practised. To accelerate the bird

colonisation in restored wetlands, a creation of artificial islets or platforms has also been used, or plantation of floating vegetation for colonial or water nesting birds (Bregnballe et al., 2014). Further on I will discuss the most used restoration measures and the ecological background of the suggested measures.

Water depth and wetland size

Water depth is an important aspect of a wetland because birds specialise on food items that can be found at different depths. Due to this niche differentiation, the wetland's bird community composition will partially depend on the variation in water depth (Sebastián-González and Green, 2014; Ma et al., 2010). Birds with longer necks or/and legs will be able to forage in deeper waters, while birds with certain bill shape that do not dive will be restricted to forage in shallow waters (Ma et al., 2010). While diving ducks (pochard *Aythya farina*, tufted duck *Aythya fuligula*, etc.) use deeper waters than most of the other wetland birds, dabbling ducks (mallard *Anas platyrhynchos*, shoveller *Spatula clypeata*, etc.) foraging on plankton and plants use mainly the shallow parts of the wetlands. Waders and herons generally use even shallower water or wet grasslands (Colwell and Taft, 2000; Noordhuis et al., 2002). Therefore it is advised to maintain a diversity of water depths also in shallow wetlands (Sebastián-González and Green, 2014; Colwell and Taft, 2000). Furthermore, too shallow waters are in the risk to dry out and thus being detrimental to the breeding success of water-dependent species (Tozer et al., 2010).

One of the most important factors for bird abundance is the size of the wetland, probably because of the increased amount of food and nesting recourses, greater habitat heterogeneity and increased connectivity with the surrounding landscape (feeding grounds) (Quesnelle et al., 2015; Ma et al., 2010; Platteeuw et al., 2010). Consequently, the density of gulls, waders and large waterfowl (but not other birds) increase with increased area of water (Sebastián-González and Green, 2014). Since diving species depend on water depth, they will not be present at small wetlands (as they are too shallow) and may abandon the wetland if it reduces in size due to the unsuitability for foraging (Ma et al., 2010; Paracuellos, 2006). If large wetlands are impossible to restore, the restoration of small wetlands is less expensive and still can be beneficial for avian communities (Stevens et al., 2003). On the other hand, it has been suggested that pesticides from farmland run-offs accumulate faster in small water bodies, thus reducing the number of invertebrates available for wetland birds (Tozer et al., 2010). Small wetlands may also offer a lower degree of conspecific and heterospecific attraction (Tozer et al., 2010), which may be important for colonisation success. Furthermore, small wetlands are generally incompatible with the home ranges of many wetland birds, such as territorial marsh songbirds, Eurasian bittern *Botaurus stellaris* and other solitary wading birds (Bancroft et al., 2002; Tozer et al., 2010; Worrall et al., 1997). This all emphasize the importance of the wetland size.

Wetland connectivity to its natural hydrology and flooding events

The restoration of flooding events in the wetlands is going to influence the habitat features and food availability for most of the wetland birds. When restoring the old drained wetlands close

to the watercourses, a common practice is to reconnect the wetlands to the main watercourse and to permit natural seasonal flooding regimes (Bregnballe et al., 2014; Gerard et al., 2008). The created dynamic water level change in time diversifies the habitat creating a hydrological mosaic, suitable for a higher variety of birds specializing in different foraging strategies (Ma et al., 2010; Źmihorski et al., 2016; Ausden et al., 2001). Some restoration programs also include the creation of shallow ditches in order to increase and better regulate the water levels in agricultural wetlands (Smart et al., 2006; Voslamber and Vulink, 2010). If restoration did not involve wetland reconnection to hydraulic flow, the wetland will have saturated water (not flowing water) that is high in nutrients and low in oxygen (O'Neal et al., 2008). Such lack of connectivity leads to a highly fluctuating water levels (water level purely depends on rainfall), which in turn can lead to a reduced germination of plant seeds, grass cover, and amount and diversity of water-living invertebrates which are the main food source for wetland birds (O'Neal et al., 2008). However, the amount of wetlands that are cut from their natural inflow and outflow varies between countries, therefore to what extent this restoration measure is needed, is hard to say.

The reconnection to a river, stream or other wetlands facilitates the dispersal of plants (for the habitat), invertebrates and fish, thus potentially increasing the amount of food for waders and other wetland birds (e.g. ducks and grebes) (Ma et al., 2010). In the response to the increased humidity in the grasslands surrounding the main wetland, the herb growth is constrained and the habitat heterogeneity is increased, positively affecting the prey availability and foraging efficiency (it is easier for waders to find prey in a humid ground than in a dry one) (Eglington et al., 2008; Źmihorski et al., 2016; Groen et al., 2012). What is more, the natural or controlled flooding is important for seed dispersal and germination, therefore flooding will benefit plants that grow in humid soils, that some of the water birds prefer to forage/forage in (Taft et al., 2002). However, when winter flooding in the UK was introduced to the previously unflooded grasslands (at least for 20 years), it actually reduced the biomass of available invertebrates, because the long-term flooding created anoxic conditions that resulted from extent organic inflow to wetlands, increasing decomposition (Ausden et al., 2001). Even though the invertebrate biomass was low, the wader foraging efficiency was actually greater there, because of the easier soil penetration and suitable feeding ground (Ausden et al., 2001).

The wet grasslands and marshes

The wader community displays niche differentiation in terms of breeding and foraging habitat preferences. Larger waders, such as curlews *Numenius arquata*, black-tailed godwits *Limosa limosa*, or snipes *Gallinago gallinago*, prefer higher vegetation with frequent tussocks to conceal their nests from predation (Durant et al., 2008). While other waders, such as northern lapwings *Vanellus vanellus* and redshanks *Tringa totanus*, prefer short ground vegetation and sparse tussocks because they nest on the open ground (Durant et al., 2008). There is no optimal vegetation height and frequency that accommodate all wading bird species, but luckily, by creating the heterogeneity in vegetation structure we may attract high densities of different breeding wader species (Durant et al., 2008; Milsom et al., 2002).

Therefore, the introduction of grazing or mowing is a typical way to restore wetland grassland for wading birds. Grazers consume dominant plants, giving the chance for the slow-growing plants to flourish in an otherwise overgrown grassland thus reducing plant competition and increasing plant diversity (Adler et al., 2001). Grazing and trampling by livestock will create a different height of vegetation increasing the small-scale habitat heterogeneity (Méró et al., 2015). The grazing animals may also respond to habitat heterogeneity, and through their food preference, maintain it (Durant et al., 2008; Adler et al., 2001). Cattle and horse grazing is thought to create heterogeneity through the explicit herb preference, horses furthermore increase it by creating patchy vegetation heights, where sheep may create a more homogenous herb height (Durant et al., 2008). Furthermore, cattle and horses prevent the overgrowth of common reed thus keeping the shoreline open and muddy for foraging waders (Voslamber and Vulink, 2010). Since some waders breed much earlier than others and have different vegetation height preferences for their nest location, the option is to adjust the grazing date depending on the breeding phenology of the wader species community (Durant et al., 2008; Smart et al., 2006). For example, autumn grazing, resulting in short vegetation at the beginning of the next spring, might be relevant for lapwings (as they prefer short vegetation and breed much earlier), while spring grazing might be more beneficial for other waders requiring higher vegetation for their breeding needs (Durant et al., 2008).

However, grazing may also have negative effects on wetland birds – as high grazing pressure can cause an increased homogeneity of short ground vegetation thus reducing the habitat suitability for birds that conceal their nest in tall vegetation. Furthermore, high grazing pressure may increase the probability of breeding failures due to the trampling of cattle (Durant et al., 2008). It is estimated that trampling by cattle can destroy 35-70 % of redshank nests (Smart et al., 2006). On the other hand, nest failures can occur not just by trampling (Smart et al., 2006), but also by the livestock disturbance that increases the risk of nest abandonment or exposure to nest predators (Durant et al., 2008). Therefore one strategy is to reduce the grazing pressures or to adjust the time of grazing (or mowing) such that the highest grazing intensity occurs outside the breeding period of most species (e.g. late summer and autumn) in order to maintain the sward structure suitable for next year's breeding (O'Brien and Wilson, 2011; Durant et al., 2008; Smart et al., 2006).

Mowing is another strategy to give a suitable nesting and foraging habitat for waders. However, mowing might not be as good as grazing, probably because mowing creates vegetation structure homogeneity (Żmihorski et al., 2016), even though mowing may still increase plant species diversity compared to unmown fields (Bucher et al., 2016). Furthermore, it has been shown that mowing (as well as intense grazing) can reduce available food (invertebrates and favourable plants) for many wetland bird species, however, the effect of such reductions for bird diversity is not known (Vickery et al., 2001). There are not so many studies looking at the effects of mowing on breeding wetland birds. However, black-tailed godwits seem to be negatively affected by mowing during the breeding season as they avoid nesting in the short vegetation (Groen et al., 2012).

Because farmland wetlands are very nutrient-rich, the consequential intense plant growth may gradually reduce the open water, especially in the first years after the restoration. As a

consequence, birds that have returned to the newly restored wetland may abandon it later on, when the foraging or nesting grounds will be lost to the high and dense grassland vegetation (Bregnballe et al., 2014). Therefore the continuous wetland management after the restorations by grazing, mowing, or reed cutting is relevant in order to avoid wetland abandonment.

Management of restored wetlands – evidence of effects on bird diversity

Even though restoration is a crucial point from where the biodiversity increase starts, constant, adaptive and goal-oriented management may be as important in order to attract, increase and maintain waterbird populations (Bregnballe et al., 2014). Most of the published wetland restoration evaluations have been focusing on grazing/mowing intensity, and regulation of water levels and flooding regimes.

Wetland depth and size

I could not find any papers directly evaluating the effects of size or depth restorations, except that overall, large wetlands can accommodate more bird species than small, while depth is very species dependent (Sebastián-González and Green, 2014). For example, the optimal restored wetland depth can successfully increase abundances of species that are of conservation concern (358% increase in Black rails *Laterallus jamaicensis coturniculus*) (Nadeau and Conway, 2015; Stevens et al., 2003). On grasslands, the amount of restored open water features positively correlated with the breeding lapwing densities (Eglington et al., 2008). However, in the habitats that cannot support large areas of restored wetlands, it has been suggested to cluster several small wetlands instead (Ma et al., 2010). This way a high habitat heterogeneity could be created that could support high bird diversity. It has been experimentally shown that complexes of several small ponds could support higher bird diversity than one pond with the same total surface area (Sebastián-González and Green, 2014; see also Smart et al., 2006). One negative effect of the restoration of water level and wetland size I could find was from the restoration of the Filsø Lake. The wetland lost over 80 % of staging pink-footed geese *Anser brachyrhynchus* during their migration, because of the flooding of their feeding site (Clausen and Madsen, 2016). Even though one would assume that wetland size and depth should be important for wetland birds, not many wetland restorations that have been researched include such restoration measures.

Grazing and mowing

A study investigating the effects of introduced grazing showed that it increased lapwing, redshank and pied avocet *Recurvirostra avosetta* densities by more than 50%, but decreased the density of oystercatcher's *Haematopus ostralegus* (Olsen and Schmidt, 2004). Another study showed a positive effect of reintroduced grazing on greylag geese *Anser anser*, shoveler and yellow wagtail *Motacilla flava*, but a negative effect on teal densities (Hellström and Berg, 2001). Several studies evaluated the effects of grazing while comparing to ungrazed wet

grasslands and found positive effects of grazing on not just wading bird diversity, but also on ducks and herons (Norris et al., 1997; Voslamber and Vulink, 2010; Mérő et al., 2015; Shrubbs et al., 1991; review by Durant et al., 2008), but may have negative effects on grebes and marsh birds, such as great reed warbler *Acrocephalus arundinaceus*, Eurasian bittern and passerines (Voslamber and Vulink, 2010). When comparing grazing or mowing, some studies suggest that grazing is a better management strategy to attract greater numbers of species, sometimes outrunning mowing by 50 % (Žmihorski et al., 2016). As for example, snipe and lapwing densities are negatively affected by restorations with mowing management (Hellström and Berg, 2001).

Some studies suggest that even low densities of livestock during the wader breeding season have a negative effect on the nest success (Hart et al., 2002). As for example in redshanks, even 0.55 cattle per hectare could directly (trampling) or indirectly (nest exposure) cause 95% of nest failures (Sharps et al., 2015). Therefore, the high-intensity grazing had substantially lower bird diversity than wetlands with low grazing pressures (Mérő et al., 2015). The reduction of grazing intensity in AES managed wetlands helped to stabilise and, in some instances increase breeding wader abundances (lapwings and redshanks, but not common snipe) (O'Brien and Wilson, 2011). Another aspect to consider is a grazing habitat preference, as it has been observed that the free-range livestock was preferring to graze in the same habitat as redshanks choose to breed, and that is why the presence of grazers can be detrimental to the breeding success of waders (Sharps et al., 2017). However, effects of grazing may be complex and perhaps context dependent. When considering redshanks, lapwings and black-tailed godwits in the Netherlands, the delayed mowing and other agricultural activities (such as fertilisation) during the breeding season have not succeeded to increase their population sizes, and in some cases, they have even declined in numbers (Breeuwer et al., 2009; Groen et al., 2012). Therefore, the effects of grazing are rather complex as grazing may have both positive and negative effects on breeding wetland birds.

Even though grazing has an effect on the breeding success, other management (e.g. flooding) could be also very effective for the bird populations (Breeuwer et al., 2009; O'Brien and Wilson, 2011). However, some of them are rarely used, because they can be incompatible with farmer's goals, such as the increase of water levels in the fields or flooding (Breeuwer et al., 2009; Eglinton et al., 2008).

Water level management and controlled flooding

Vast areas of natural flooding may have strong negative effects, as nests may get under water and food availability may be drastically reduced. Therefore flooding should be controlled to vary within certain levels in order to maintain a heterogeneous and food rich environment increasing the wader population numbers (Eglinton et al., 2008). Actually, the high levels of flooding may push waders to nest at the edges of wetlands in order to avoid nest drowning, which in turn may expose nests to mammalian predators (Laidlaw et al., 2017). Therefore wetland flooding should be managed according to the requirements of a specific wetland.

Studies suggest that the flooding in wetland grasslands increase species richness and abundance of several species groups of wetland birds and that flooding regime interacts with other management strategies, such as the degree of wetness and grazing or mowing, as shown in *figure 1* (e.g. waders; Źmihorski et al., 2016). In Scotland, the fields that had increased flooding compared to the reduced grazing intensity management had less breeding waders. It is probably because wet grasslands in such farmlands lack grazers throughout the year, therefore the habitat there becomes homogeneous and unsuitable for waders (O'Brien and Wilson, 2011). A general pattern is that wader densities increase by the increased mosaic of water features and maintenance of basic levels of humidity (Eglington et al., 2008). The concentrated flooding (increasing water levels, but not flooding the grasslands) was shown to increase lapwing and redshank breeding densities through nesting habitat provision (Laidlaw et al., 2017). The controlled and adjusted wetland flooding can successfully increase the foraging efficiency for waders (Ausden et al., 2001; Groen et al., 2012). Wetlands linked to natural hydrologic systems can support higher migrating and wintering bird diversity compared to isolated ones (Xia et al., 2016). Actually, isolated water bodies may not be able to sustain a permanent high abundance of birds due to the effects of local exhaustion of invertebrate prey (Almeida et al., 2017). A 10-20 cm flooding of wetlands appears to be the most suitable to accommodate the most of the wetland species, as the different depths of water can be used by different taxa (Colwell and Taft, 2000). The restored wetlands with natural water flow can have 400 % higher waterfowl richness compared to the non-flooded ones (O'Neal et al., 2008). Such a drastic difference could be seen probably because the non-flooded wetlands in this study area often dried out, where flooded wetlands were more stable in terms of water availability (O'Neal et al., 2008).

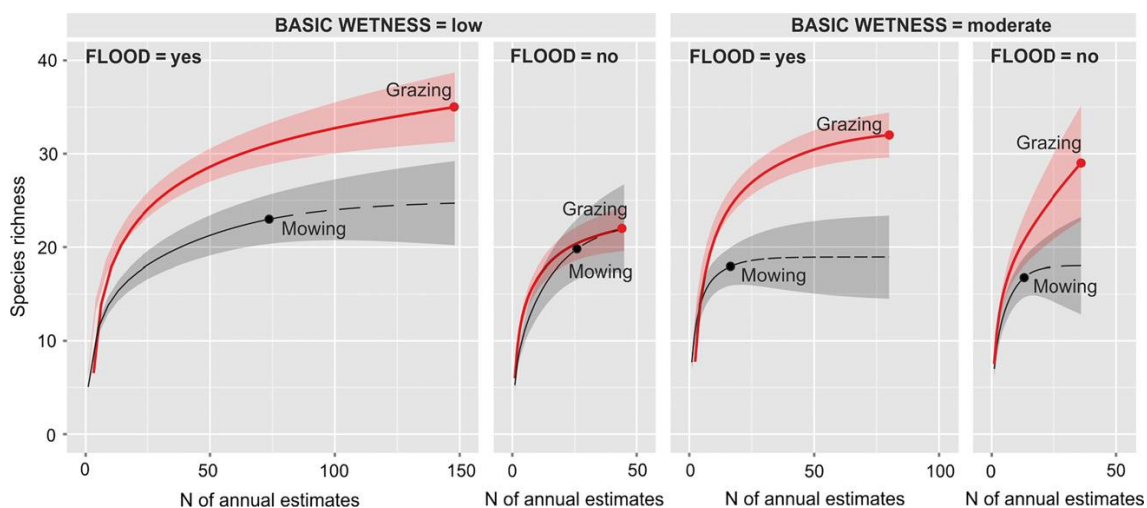


Figure 1. The estimated wet grassland bird richness depending on (i) low or moderate basic wetness, (ii) presence or absence of flooding regimes, (iii) grazing or mowing management regimes. Transparent polygons denote 95% CI for each curve, dots denote observed species richness, and dashed curves represent extrapolated species richness. Adapted from Źmihorski et al., 2016.

In conclusion, there is a general lack of studies directly measuring the effects of wetland restorations, e.g. studies evaluating the bird populations before and after the restoration. It is probable that the evaluations of wetland restorations are often in the shape of reports that are

not reaching a wider public. The few studies that evaluated the effects of wetland restoration in comparison to unrestored wetlands show positive effects of grazing and flooding, but grazing had also some negative effects that could be reduced with appropriate management. Furthermore, many studies are case studies, therefore the results discussed here are generally location dependent rather than evaluating large-scale patterns.

Restoration, management and species interactions

The implemented restoration measures will affect parts of the wetland bird communities in a species-specific way due to the changed habitat structures and species-specific niches. What is much less investigated is whether the restoration measures also affect species interactions, or whether it may cause trophic cascades in the local wetland bird community. To my knowledge, there are no studies on restoration-driven trophic cascades in wetland bird communities, but several studies have investigated the effects of competition, attraction, facilitation, and predation on the occurrence of wetland bird species. However, how these interactions are affected by wetland restoration measures is generally not known, with the possible exception of some studies on predation.

Predation

Most management strategies focus on the provision of suitable nesting spaces and foraging habitat, but much less so on the habitat features affecting predation risks (Laidlaw et al., 2017). Some of the wetland management strategies may have an effect on predator-prey interactions. Predation during the breeding period decreases the nesting success (Laidlaw et al., 2017), and thus may potentially limit the recovery of bird populations in restored wetlands (Malpas et al., 2013). One way to avoid predation is to manage habitat in a way that generalist predators would have other preferred prey than wetland birds (Laidlaw et al., 2017). For example, maintain patches of tall grasslands which are preferred habitat for small mammals, which are preferred prey for red foxes (Laidlaw et al., 2017). Another option is to manage the wetlands in a way that it is most suitable for the high densities of breeding wader (or gulls and terns) species that actively protect themselves against flying and terrestrial predators through intense mobbing behaviour so that the other species would benefit from it (Laidlaw et al., 2017). The third intervention is the physically fencing from terrestrial predators by any types of fences, which could reduce predation rates of lapwing nests and chicks, especially the electricity-powered fences (Malpas et al., 2013), but such management has no effect on avian predators.

The fourth predator control could be active killing, which in itself is a rather controversial and time-consuming (Malpas et al., 2013). Moreover, the active control of the red fox and carrion crow may not actually have any effect on wader populations (e.g. Bolton et al., 2007), as there were high immigration rates. And such management requires eradicating a large portion of predators in order to be successful (Smith et al., 2010). Furthermore, the active killing is usually used to regulate the larger predators, which can, in turn, lead to the increase of mezzo-predators (Malpas et al., 2013).

Waders, such as snipe, conceal their nests in high vegetation and have plumage that makes them cryptic in order to prevent nest predation (Durant et al., 2008). Therefore the management or restoration of wetlands in a way that it would create habitat structures favoured by wetland birds and that somehow protects them from predators are relevant. When considering the bird colonies, they are visible and impossible to conceal, therefore they choose to breed on islands or trees that would help them to avoid predation (Platteuw et al., 2010), therefore creation or restoration of islands and presence of some trees may be relevant for colonial species, such as herons. The perceived risk of predation has an effect on the process of breeding habitat selection. For example, waders will avoid breeding close by human-made structures (alternatively also close by trees or forests) in agricultural wetlands, because those structures attract crows that may use these look-out structures for finding nests (Wallander et al., 2006; Berg et al., 1992). What is more, high water levels create fragmented water structures that may be a way to constrain mammalian predators to move, as they tend to avoid water. Therefore such structures can reduce nesting wader predation of the nests that are surrounded by water (Laidlaw et al., 2017; Smart et al., 2006). However, high levels of flooding may push waders to nest on the edges of wetlands (in order to avoid nest drowning), which in turn exposes nests to predation (Laidlaw et al., 2017). All these findings show that habitat structures will have an effect on predator-prey interactions and thus will modify the outcomes of wetland restorations.

Competition and attraction

A bird's decision to select a breeding habitat may depend on the assessment of habitat quality as estimated by visual environmental cues and/or by the presence of other individuals or species, so-called social cues (Sebastián-González et al., 2010). It is possible therefore that restored habitats remain unoccupied, even though they offer suitable environment (Fletcher, 2008), or that the wetlands with similar features have different community structures (Bayard and Elphick, 2012; Ward et al., 2010). In this section, I will review studies investigating species interactions among wetland birds, and reflect upon which results and findings may be relevant when evaluating the effects of farmland wetland restorations for bird diversity.

Conspecific competition vs. attraction

Conspecific facilitation, attraction, and competition may all have an effect on whether a species will inhabit and colonise a restored wetland. However, it is hard to find any studies investigating the restoration effects of conspecific interactions in wetland birds. In theory, the increased densities should increase the competition for food or nesting sites (Osnas, 2003). However, the few studies evaluating the conspecific food competition are conducted during the non-breeding period. For example, increasing local numbers of conspecific waders tend to negatively relate to individual feeding rates (oystercatchers, redshanks) (Goss-Custard, 2002). Furthermore, increased numbers of waders will force some conspecifics to forage at lower quality patches (Goss-Custard, 2002). The related species may respond differently to the increased numbers of conspecifics: red knot *Calidris canutus* feeds on the undesirable food items and spend more time being vigilant, where ruddy turnstones *Arenaria interpres* decrease feeding rates (Vahl et al., 2005). In general, the role of competition is a rather hard topic to test in waterfowl because of the difficulty to measure the intake and abundances of food (Goss-

Custard, 2002). Therefore the conspecific competition may be affected by restorations just in those cases when food availability is low, for example, in the wetlands that do not have natural hydrology.

Other studies about the intraspecific competition in wetlands are related to nest parasitism (Åhlund, 2005; Lank et al., 1989; Semel and Sherman, 2001). For example, female common goldeneyes *Bucephala clangula* lay eggs in conspecific nests that have not been predated in the previous years (Pöysä, 2006). The nest parasitism within waterfowl maybe also connected to the relativeness, where parasitized birds gain inclusive fitness (where hosts with low fecundity help related parasites) (Andersson, 2017; Eadie and Lyon, 2011). Therefore, nest parasitism is unlikely to occur due to the competition for nesting sites (Åhlund, 2005). In barnacle geese *Branta leucopsis*, for example, the parasitic nesting behaviour occurred in the year they did not nest, showing a case of an alternative reproductive strategy (Forslund and Larsson, 1995). However, whether conspecific nest parasitism has an effect on the total output of young from a wetland and whether it is linked to restoration measures are generally not known.

Conspecific attraction could be beneficial because of (i) the increased probability of finding a mate (Coulton et al., 2011), (ii) facilitated breeding habitat selection (Parker et al., 2007), (iii) the reduced risk of predation because of communal defence, as e.g. in lapwings (Berg et al., 1992). Lapwings actively protect themselves against flying and terrestrial predators through mobbing behaviour, and higher lapwing densities significantly decrease their nest predation (Laidlaw et al., 2017). Black-headed gull *Chroicocephalus ridibundus* and common tern *Sterna hirundo* colonies also successfully protect themselves from crow predations (Väänänen, 2000). However, due to the increased risk of the intraspecific nest predation, the black-headed gulls will stop such a defensive behaviour against predators with the increased colony densities (Kruuk, 1964).

Only a few studies in wetland birds have investigated whether the colonisation of new patches is facilitated by conspecific attraction. These studies suggest the action of conspecific attraction in some colonial seabirds, such as terns, common guillemots and kittiwakes and in some songbirds in restored wetlands (Bayard and Elphick, 2012). Conspecific density may be used as a habitat selection cue signalling habitat quality, as it may reflect social and environmental factors (Bayard and Elphick, 2012; Parker et al., 2007). The conspecific density cue-dependent immigration to a breeding habitat was recorded in Eurasian spoonbill *Platalea leucorodia* and female mallards (Tenan et al., 2017; Coulton et al., 2011). Therefore conspecific attraction is an important factor to consider when evaluating the effects of wetland restoration on the species abundances and presence. In general, we expect either delayed or increased effects of restorations when the conspecific attraction is important in habitat selection decisions, thus increasing the variation in the outcomes.

Few studies have experimentally shown that conspecific social cues (density-dependent) will determine the habitat selection for the next year's breeding, and in some cases, such cues are even more important than habitat suitability (Nocera et al., 2006; Betts et al., 2008). In the great cormorant *Phalacrocorax carbo* the breeding age, dispersal probability and immigration

depended on the conspecific breeding success in the previous years (Frederiksen and Bregnballe, 2001; Henaux et al., 2007). These decisions could result in colonial aggregations in wetland birds (Danchin et al., 1998). Therefore the immigration, emigration and recruitment rates could potentially indicate the wetland restoration success on the breeding conditions of wetland birds.

Heterospecific competition and avoidance

The negative interactions between species may shape the wetland bird community. Two competing territorial grebe species could only co-exist in high-quality large wetlands because in small-sized wetlands the negative effects of interspecific aggression limit the number of nesting sites for one species (Osnas, 2003). Clearly, the heterospecific competition may structure the wetland bird communities and restrict which species may colonise after a restoration measure. Heterospecific competition is expected to be highest in small-sized wetlands, as in conspecific competition, and increase with increased densities (Goss-Custard, 2002). However, to what extent the interspecific competition affects the species co-occurrence has generally not been investigated in wetland bird communities.

Wader species tend to co-occur together even though they share similar niches, showing that wetland ecosystems can offer sufficiently high food availability (Sebastián-González et al., 2010). A study with co-existing waders in a stopover site in China showed, that 3 wader species have a high overlap in their diets, proving that high food availability rather than niche separation enables them to co-exist (Choi et al., 2017). On the other hand, dabbling ducks, in this case, mallard, teal *Anas crecca* and pintail *Anas acuta*, have a complete food preference separation throughout all the seasons showing niche differentiation that enables these competing species to co-exist (Brochet et al., 2012 review). Another study showed a lack of competition between the breeding mallard and teal (Elmberg et al., 1997). Yet, one study claimed that dabbling ducks tend to have skewed heterospecific niche separation when food is abundant and more pronounced when food is constrained (wintertime), showing seasonal variation (DuBow, 1988). Another study claimed that diving and dabbling duck species co-existence within guilds depends on their body size and the total niche space of the habitat (Nudds, 1983). A study on the wetland hemi-marsh bird co-occurrence did not find any support for heterospecific exclusion (Ward et al., 2010). Therefore it appears, that food availability may determine the level of heterospecific competition. The heterospecific competition is a rather difficult interaction to investigate due to the high availability of food. The effects of heterospecific competition on the occurrence and abundance of wetland birds are therefore most likely to be present in small wetlands of territorial bird species (as the breeding space and food availability may be more limited there). All in all, the wetland productivity through flooding and appropriate management will have the most significant effect on the heterospecific co-existence in the restored wetlands, as it will directly affect the food availability.

Heterospecific attraction

As mentioned above, the heterospecific competition is a rather controversial topic, even though competition between co-existing species are assumed to have a high influence on the species

co-occurrence (Mönkkönen et al., 1990). Actually, the heterospecific attraction but not competition can have a strong influence on forming the songbird communities (Mönkkönen et al., 1990). The social information provided by the presence of interspecific with similar niche may be used by the colonising and migratory birds in order to estimate the habitat quality (food abundance, safety, etc.) (Thomson et al., 2003; Sebastián-González et al., 2010; Ward et al., 2010). Social information can even be used by the heterospecifics for choosing the next year's breeding site based on the nest success of heterospecific (Parejo et al., 2005), showing the ways that heterospecific provided information can be used in the settling decisions. Only very few studies have been done investigating the heterospecific attraction in the wetland bird communities, and none in a relation to the farmland wetland restorations.

One study showed that the wetland bird species co-occurrence in the irrigation ponds is not random, but rather related to heterospecific attraction (Sebastián-González et al., 2010). Wetland species tend to aggregate within ponds, even though there are unoccupied surrounding ponds available (Sebastián-González et al., 2010). The authors admit that there may be environmental variables that were not included in the analyses that could influence the species aggregations, but the effect of heterospecific attraction is evident, because multivariate analyses in this study was accounting for the known environmental variables influencing the bird occurrences and was based on time series data (Sebastián-González et al., 2010). An experimental study with dabbling ducks showed that heterospecific attraction influenced the settlement decisions, independent of the water body size or habitat heterogeneity (Elmberg et al., 1997). Wetland species that are the most frequently co-occurring with the other ones are also the first ones to arrive at the breeding sites (Ward et al., 2010). It was suggested that this species (pied-billed grebes *Podilymbus podiceps*) may be chosen by the heterospecifics as a habitat selection cue due to the high abundance, early breeding time and a rather active vocalisation (Ward et al., 2010). Therefore identifying the species that are used by the heterospecifics in their habitat selection choices could help to facilitate the diverse colonisation of birds in the restored wetlands. Restored wetlands that can attract (by management, restoration measures or by the use of decoys and vocalisations) the birds that are used as social cues by their heterospecifics could significantly improve the wetland restoration outcome for bird diversity. On the other hand, species that co-occur with one species tend to co-occur with another species as well, suggesting that species that are attracted by heterospecifics may cue for a type of bird community rather than specific species itself (Ward et al., 2010) further on complicating our understanding about the species interactions.

To continue, the presence of conspecifics may have an effect on the predation risk that is recorded in a few waterbird species. The increased lapwing densities also decreased the probability of redshank nest predation, however, this effect was not disentangled from the decreased predation risk simply by diluting such effect of increased densities (Laidlaw et al., 2017). Pochard and tufted duck species in Finland breed tightly with the black-headed gull and little gull *Larus minutus* colonies and that they had lower predation rates in the gull colonies compared to the outside colonies (Väänänen et al., 2016). Actually, a decrease in the tufted duck and pochard populations has been suggested to be dependent on the decrease in the black-headed gull colonies (Väänänen, 2000). Therefore, wetland restorations may need to consider

some particular restoration measures to attract and support high numbers of such key species that can protect heterospecifics from predation. If such protective species are absent, the wetland may fail to maintain viable populations of these species. On the other hand, gulls may predate duck nests within the colony as well, creating an ecological trap, therefore terns may be a better heterospecific to attract in order to reduce duck nest predation, as terns do not predate nests (Dwernychuk and Boag, 1972).

Another interesting example of heterospecific indirect nest protection is of curlews and kestrels *Falco tinnunculus*. Curlews prefer to build their nests close to the kestrel nests, which are their nest predators (Norrdahl et al., 1995). Even though kestrels are partially responsible for the curlew nest predation, the curlew nests that were close to kestrel's had lower predation rates than nests away from them (Norrdahl et al., 1995). This all supports that heterospecific presence may have high benefits even though it also has some costs when considering some species interactions. When considering the effects of wetland restorations on waterbird communities, one must take into the account that restoration measures will have an effect on the direct and indirect predator-prey dynamics and heterospecific interactions and that such interactions, in turn, may also have an effect on the outcomes of the wetland restoration and management.

All in all, it is hard to predict how the species interactions can affect the bird community in restored farmland wetlands, e.g. how the species interactions interplay with the wetland restoration measures on bird diversity. Even though there are too few studies to start to base our thinking on such evaluations, negative interactions could decrease the wetland bird richness and abundances, while positive ones could increase it. Furthermore, the species diversity would not vary as much between similar, close located wetlands. Therefore a good starting point could be a comparison of species co-occurrences and diversity indexes, which, after accounting for environmental variables, could give us an idea about the role of species interactions in restored wetlands.

Conclusions and future research

It seems that the current research shows that the most important restoration measures are the ones that indirectly or directly affect the bird's breeding and foraging efficiency. Increasing wetland size can likely increase the wetland bird abundances and species richness, but increasing wetland size may be unrealistic to do due to the high costs. Water depth is an important factor linked to the niche separation of species, thus a diverse water depth within the wetland may increase bird diversity. The flooding of wetlands will also diversify habitat which will increase the suitability for the higher diversity of birds, but flooding has to be controlled as it may have strong negative effects on birds at high levels of flooding. The grazing of wet grasslands tends to improve the habitat for several wader species but it may also have negative effects (failures due to increased risk of trampling, exposed nest to predators). Even though there are studies evaluating such restoration effects on birds from local and landscape scales, just a few of them are not case studies. Also, we are lacking the studies that are evaluating the effects of wetland restorations while comparing the bird diversity before and after the

restoration. Furthermore, some restoration measures may work for one species, but not for others, especially for the species of conservation interest. Therefore an adaptive management could increase the targeted species population through constant monitoring and management improvement (O'Brien and Wilson, 2011; Perkins et al., 2011).

Sometimes a restored wetland may stay unoccupied by birds or be occupied by only a few species and at low abundances, even though it has all the environmental variables that are thought to increase the bird diversity, and wetlands with similar features and management have very different bird communities. This can be due to three things. Firstly, the factors that are affecting the bird's decision to reside within a wetland is not known (e.g. landscape composition, abiotic variables, etc.). Secondly, the effects of the wetland restoration and management can increase the bird diversity in the surrounding wetlands due to emigration from the restored one and immigration to neighbouring wetlands (Breeuwer et al., 2009). Therefore the effects of restoration will not be visible in the restored wetland itself but only at a larger spatial context of several neighbouring wetlands. Thirdly, the species interactions may be responsible for the presence or absence of the wetland birds.

Even though there are not many studies that are investigating the effects of wetland restorations on species interactions, the few published ones still look promising. A study with waders showed that flooding and the complex open water mosaic had decreased the predation rates by terrestrial predators (Laidlaw et al., 2017), which should increase the wader populations. I would then also expect the grazing management to have an effect on the predation rates of wader nests, as, for example, the previously concealed nests could be exposed to predators. Or that the grazing management could attract higher abundances of birds, such as lapwings, who are using the mobbing behaviour against predators (and more birds protect better than a few), that could also attract heterospecifics that may benefit from lapwing protection against predators. There may also be species which decide to reside in a given location not only by the suitable landscape features but also by the presence of conspecifics or heterospecifics. Therefore the knowledge about the species interactions and how they can be affected by wetland restorations could help us to understand what affects the wetland bird community structure and what could improve the efficiency of wetland restorations.

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