



Populations in stable and variable habitats: Green and common sandpiper in a beaver-influenced landscape

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ABSTRACT

Stability of breeding habitat use and population variability was studied in two common wader species: green sandpiper *Tringa ochropus* and common sandpiper *Actitis hypoleucos* in a boreal lake area in southern Finland. The main natural driver of habitat disturbance in the area is an ecosystem engineer, the North American beaver *Castor canadensis*. We also studied the presence and abundance of green sandpipers before, during and after beaver-induced floods.

In the studied landscape, the variable habitat created by beaver flooding appeared to have carrying capacity for a larger green sandpiper population than the more stable habitat for that of the common sandpiper. Common sandpipers made much use of the same lakes from year to year whereas the occupation of wetlands by the green sandpiper was more variable. The population of common sandpipers fluctuated more, although they inhabited the more stable environment. Green sandpiper pair numbers increased during beaver flooding, which suggests that they adapt rapidly to changes in breeding site availability. Some of the facilitating effects of the beaver appeared to remain 1–2 years after the flooding.

1. Introduction

Environmental predictability in habitat availability exercises a selective pressure on animal behavior. Temporal availability of habitat also drives animal movement (Lambert and Matthiopoulos, 2020); accordingly, it has been noted that habitat stability leads to site fidelity whereas in variable habitats animals tend to switch their breeding place (Switzer, 1993). Furthermore, environmental patterns can differ in terms of predictability at different temporal and spatial scales (Orians and Wittenberger, 1991; Lambert and Matthiopoulos, 2020). To be able to predict the temporal access to a high-quality breeding site or a food resource might lead to an improved breeding success or survival. According to Southwood (1977), the probability of finding a new suitable breeding habitat depends mostly on spatial characteristics, such as the distance between habitats, size of habitat patches and the migratory range of the organism (also Schooley and Wiens, 2003; Kokko and López-Sepulcre, 2006). New habitats might provide better resources and fewer natural enemies.

In the boreal area, seasonal variability in habitat accessibility is an important factor determining temporal diversity in different habitat types (Dalby et al., 2014; Holopainen et al., 2015). Among these habitat types, wetlands play a significant role in regional bird diversity (Salmela et al., 2007). Wetlands are essential breeding grounds as well as feeding and resting sites for many species, such as waterbirds and waders (Tiainen et al., 2016). Boreal lakes are morphologically stable especially at the landscape level (Shorohova

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et al., 2009; Pöysä et al., 2016). Changes at different scales might nevertheless be caused by natural disturbances and anthropogenic factors (Suhonen et al., 2011; Alahuhta and Aroviita, 2016). In the boreal wetlands, beaver is an important driver of patch disturbances (Remillard et al., 1987; Nummi and Pöysä, 1997; Kivinen et al., 2020).

Beavers alter their surroundings mainly through dam building, thereby changing the hydrology, biogeochemistry, and geomorphology of ecosystems, as well as influencing species assemblages (Naiman et al., 1986; Stringer and Gaywood, 2016; Nummi et al., 2018). Beavers, as ecosystem engineers, facilitate not only individual species (Nummi and Hahtola, 2008; Bartel et al., 2010), but whole communities of species as well (Dalbeck et al., 2007; Nummi and Holopainen, 2014). They have a strong impact on the environment by affecting the availability and quality of wetlands (Johnston and Naiman, 1990; Hood and Bayley, 2008; Kivinen et al., 2020). Hence, these ecosystem engineers provide new breeding habitat to several waterbird species by flooding, which leads to higher waterbird diversity in beaver ponds as compared to other habitat types (Nummi and Holopainen, 2014). As a disturbance factor of boreal landscapes, flooding by beavers is more predictable than e.g. fire or storms (Nummi and Kuuluvainen, 2013). Therefore, the presence of beavers at a landscape scale might facilitate waterbirds – as has been shown for the common teal *Anas crecca* (Nummi et al., 2019a, 2019b). However, on a patch scale beaver activities lead to uncertainties in where and when these favourable breeding habitats will be available.

Stability of the environment is known to affect the habitat use of many bird species, such as several ducks (Nudds, 1983; Bethke and Nudds, 1993; Suhonen et al., 2011; Holopainen et al., 2014; Nummi et al., 2015). Very little research on wader habitat requirements have been done on the boreal forest breeding grounds. More specifically, even less is known of the habitat use, and of the role of habitat variability in it, of the common sandpiper *Actitis hypoleucos* and green sandpiper *Tringa ochropus* during the breeding season. These species were reported having high site-fidelity on either breeding (common sandpiper, Holland et al., 1982) or wintering (green sandpiper, Smith et al., 1992) grounds in the temperate areas of England. Nevertheless, green sandpiper was found colonizing newly created habitats quickly at breeding areas (Nummi and Holopainen, 2014), and also sometimes shifting habitats at wintering sites (Smith et al., 1992). The effect of beaver-induced floods as well as before and during flooding has been studied in ducks but not in detail in waders. Beaver ponds, as compared to non-beaver ponds, have higher production of invertebrates from which many species benefit, as demonstrated for the common teal (Nummi and Hahtola, 2008). Both common and green sandpiper are also known to feed on a variety of invertebrates (Yalden, 1986; Ormerod and Tyler, 1988). Thus, we can predict that beaver ponds might be attractive to these species as breeding sites.

The aim of this research was to study the stability of habitat use as well as population density and variability of green and common sandpiper. Additionally, we tested the effect of flooding by beavers on sandpipers by assessing their presence before, during and after flooding events.

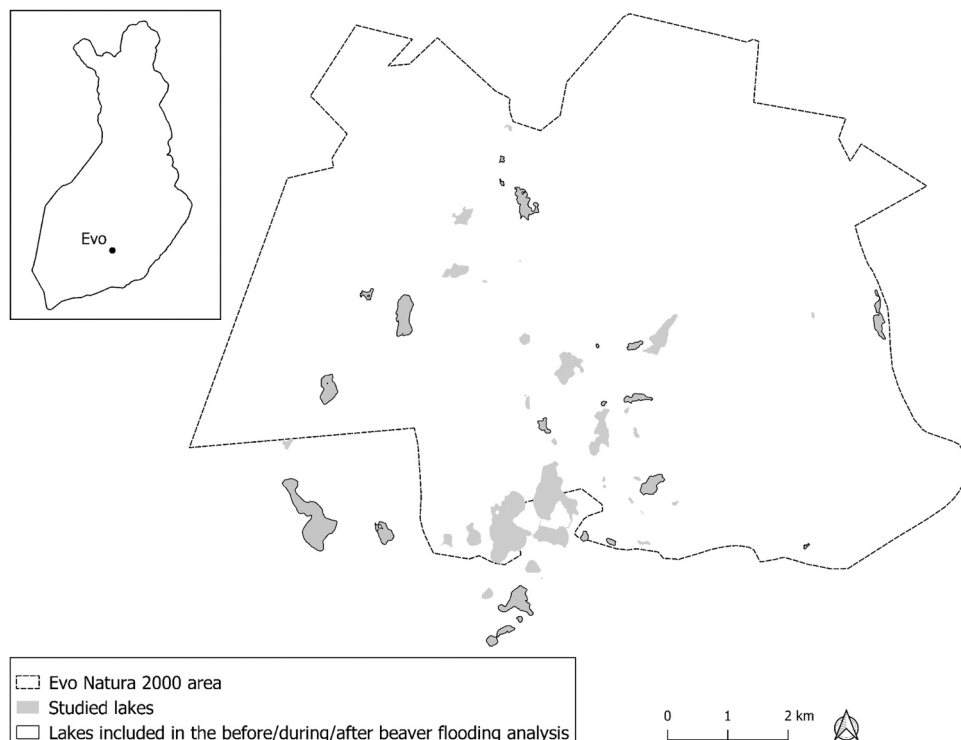


Fig. 1. Location of the study sites within the Evo Natura 2000 area, southern Finland.

2. Materials and methods

2.1. Site description

The study area consists of 52 mixo-oligotrophic lakes and ponds in the Evo-region (Arvola et al., 2010), southern Finland (Evo Natura 2000 area: 61°120'N, 25°070'E, Fig. 1). The Evo area is sparsely populated. It is covered by typical boreal coniferous and mixed forests, mostly in commercial use for timber harvesting. The shores of wetlands – lakes and ponds – usually are steep and often surrounded by mire vegetation, but sometimes forests growing on sandy soils extend up to the shore (Nummi and Pöysä, 1993; Holopainen et al., 2014). During the course of the study, 25 lakes were flooded by beavers and 22 of them were followed to specifically assess the impact of beaver on the abundance of waders.

2.2. Bird surveys

To study the habitat use stability, the two wader species, common sandpiper and green sandpiper, were surveyed from 1989 to 2008 at the 52 wetlands. On a general level, common sandpiper is slightly more common in Finland (numbering 180,000 pairs) than green sandpiper (150,000 pairs) (Lehikoinen et al., 2019). The bird surveys were performed thrice annually: in early May, and in early and late June as a combination of point and round surveys (Koskimies and Viisinen, 1991). Point surveys consist in recording all individuals observed from predefined locations along the shoreline, while round surveys consist in recording all the birds observed along a predefined route. Point surveys were performed from shore and round surveys circling the lake by foot, canoe or boat (see Nummi and Pöysä, 1993; Nummi and Holopainen, 2014).

The data used to assess the use of beaver sites by sandpiper before, during, and after flooding was collected from 1989 to 2014. It consisted of four surveys carried out in early May, early and late June as well as early July. Common sandpipers were too rarely observed at these sites to allow a comparison of the use before, during and after flooding by beavers. Only green sandpipers yielded enough data for before, during, and after use of these habitats.

2.3. Beaver occupancy

The beaver species in Evo region is North American beaver *Castor canadensis* which were introduced to Evo in 1957; the indigenous *C. fiber* had been exterminated from the area a few centuries earlier (Lahti and Helminen, 1974; Parker et al., 2012). Both beaver species are assumed to build in a similar way (Danilov and Fyodorov, 2015). Nowadays, beavers are commonly occurring in the area. The beaver occupation in Evo in a wetland is generally short-term: beavers will inhabit a site for approximately three years in a row (Kivinen et al., 2020). Beavers also seem to return to sites they have inhabited earlier; according to Hyvönen and Nummi (2008) beavers returned after nine years, on average. Beaver occupancy and flood were checked yearly in the study lakes during waterbird surveys.

2.4. Statistical analyses

2.4.1. Comparison of pair densities

Pair density was calculated as the number of pairs divided by the shoreline lengths for each wetland in order to take account for differences in lake surface. The survey with the highest number of observations per year was used to estimate density of breeding pairs for each wetland. Based on these densities, the annual average density for the area per year was calculated and subsequently used in the analyses. The pair densities of the two species followed a non-normal distribution (Shapiro-Wilk's test, common sandpiper: $W = 0.436$, $p < 0.001$, green sandpiper: $W = 0.821$, $p < 0.001$), thus they were compared with the Mann-Whitney U -test. The coefficient of variation (CV), which shows the standard deviation from the mean, was also calculated.

2.4.2. Comparison of lake use

The Sørensen's quotient of similarity (QS) index was used in the comparison of the year-to-year similarity of wetland use of these species. The yearly presence-absence of the species was used to calculate the Sørensen index. The Sørensen quotient gives index values between 0 and 1, the latter meaning greater similarity. These indices, which followed a normal distribution (common sandpiper: $W = 0.962$, $p = 0.603$; green sandpiper $W = 0.964$, $p = 0.658$), were then compared with paired-sample t -test.

The use of wetlands of different sizes by the two species was studied by comparing the average highest number of pairs per wetland from 1989 to 2008 and the shoreline length with Spearman correlations.

2.4.3. Comparison of green sandpiper abundance before, during and after beaver flood

To compare green sandpiper abundance before, during, and after beaver flooding, we used two-year periods when possible, to have two years before, two years during and two years after the beaver flood. The two-year period was based on the earlier observations noting the response of ducks to flooding during the two first flood years (Nummi and Pöysä, 1997; Nummi and Holopainen, 2014). If the area remained flooded only one year, one-year periods were used instead (Nummi and Holopainen, 2014). The number of green sandpiper pairs was collected as a sum of four bird surveys per year to investigate the habitat use of the birds. Beaver flooding had been observed in 25 of the 52 lakes during the time frame used in this study. Out of these 25 lakes, 22 lakes could be used in the before, during, and after comparison, i.e. 3 lakes were excluded from the analysis because they were flooded by beaver at the beginning of the

wader survey and therefore no information on the “before flooding stage” was available for the analysis.

A Friedman test was used in establishing the effect of the three different flood categories on the number of green sandpiper pairs. The dependent (response) factor was the number of green sandpiper pairs per study site. The explanatory variable was the status of beaver flood with the three following categories: before, during and after beaver flood. The Friedman test was followed up by pairwise Wilcoxon signed-rank tests for identifying which groups are different. p -values were adjusted using the Bonferroni multiple testing correction method.

The data were processed with R software (version 4.0.3, R Core Team, 2018).

3. Results

The average pair density calculated from the annual mean densities 1989–2008 for the common sandpiper was 0.14 ($SD = 0.09$) pairs per shoreline kilometer, which was significantly lower than that for the green sandpiper, 0.40 ($SD = 0.14$) pairs per shoreline kilometer ($W = 379$, $p < 0.0001$, Fig. 2). Pair density of green sandpiper was higher than pair density of common sandpiper throughout the 20-year study period except for the first year, 1989 (see Fig. 2). The coefficient of variation (CV), calculated from the pair densities for the common sandpiper was ~ 0.66 and ~ 0.36 for the green sandpiper.

Comparison of Sørensen indices for these species showed that the annual habitat use of the common sandpiper was more stable than that of green sandpiper (paired-samples t -test: $df = 18$, $t = 3.966$, $p < 0.001$). Mean ($\pm SD$) Sørensen index for common sandpiper was 0.62 (± 0.11) and for green sandpiper 0.45 (± 0.15). During the 20-year observation period, common sandpipers seemed to make much use of the same lakes, while the wetland use of green sandpipers was more variable. Green sandpiper was never observed at ten of the 52 wetlands during the course of the study, while common sandpiper was found to be continuously absent from 25 of the study sites. The stable habitats that common sandpiper preferred were larger lakes whereas green sandpipers occupied smaller wetlands (Spearman, $r_s = 0.74$, $p < 0.0001$; $r_s = 0.05$, $p = 0.73$ respectively).

The number of green sandpiper pairs was significantly different depending on the flooding stage (Fig. 3, Friedman test, $n = 22$, $\chi^2(2) = 7.85$, $df = 2$, $p = 0.02$). Nevertheless, the effect size is small (Kendall's $W = 0.178$). Pairwise Wilcoxon signed rank test between groups revealed statistically significant differences between before and during flooding episodes ($p = 0.028$), but neither between before and after flooding ($p = 0.119$) nor between during and after flooding ($p = 0.981$). The number of green sandpiper pairs was highest during the presence of water over time due to flooding by beavers, and stayed relative high also after the water levels subsided (Fig. 3). Green sandpipers were observed on 21 beaver-flooded wetlands from a total of 22 lakes during the course of the study.

4. Discussion

It is interesting to note that in our study area in boreal Finland, the carrying capacity of the variable habitat for green sandpipers appeared to be higher than the carrying capacity of the more stable habitat for common sandpipers. But in order to have this kind of variability in the landscape, there has to be factor of disturbance. This factor is beaver flooding. With its ecosystem engineering, the beaver acts as facilitator for the green sandpiper by increasing the invertebrate production of wetlands and creating shore areas of shallow water (Beard, 1953; Nummi and Hahtola, 2008; Nummi and Holopainen, 2014). There is also abiotic variability in the studied landscape caused by the melting of snow (Holopainen et al., 2014), but their area and effect are more limited, at least during the present time (Nummi et al., unpubl.). In a similar landscape without beavers in Nuukio in southern Finland, the density of green

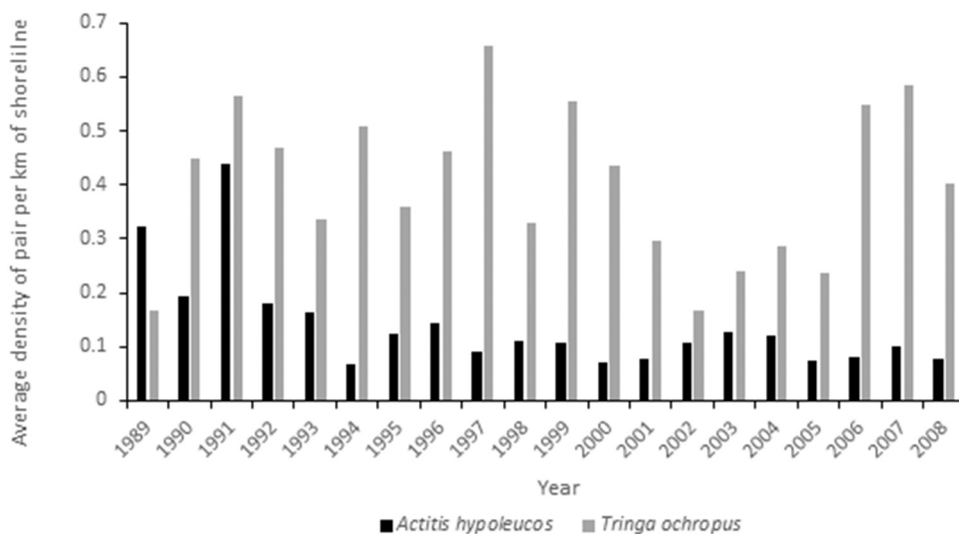


Fig. 2. The annual mean densities of the common *Actitis hypoleucos* and green sandpiper *Tringa ochropus* per kilometer of shoreline, in the study area during 1989–2008, based on the 52 study sites.

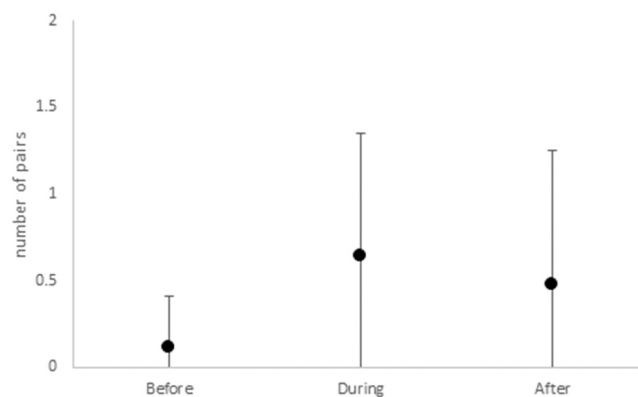


Fig. 3. Mean \pm SD number of pairs of green sandpiper *Tringa ochropus* before, during and after flooding of 22 wetlands by beavers.

sandpipers is much lower than in Evo (Nummi and Väänänen, unpubl.); the situation is similar to what has been shown in these same landscapes for the common teal, which also is beneficially influenced by wetlands modified by beavers (Nummi et al., 2019a). In the beaverless Nuukio, the common sandpiper also is more numerous than the green sandpiper (Nummi and Väänänen, unpubl.).

It is peculiar that the population of green sandpiper, which lives in a variable environment, seems to be more stable than the population of common sandpiper living in a more stable environment. It is not clear what causes this pattern, but one possibility is that the ground-breeding common sandpiper is more affected by mammalian mesopredators than the green sandpiper, which nests in trees. Another wader, the lapwing *Vanellus vanellus*, which similarly as the common sandpiper has its nest near the shoreline or among short vegetation, is shown to be prone to predation, whether by alien raccoon dogs *Nyctereutes procyonoides* (Nummi et al., 2019b) or indigenous foxes *Vulpes vulpes* (Bolton et al., 2007). Common sandpipers might also be affected by developments in the wintering grounds where they have faced declines (Bird Guides, 2018).

The use of different kinds of habitats of these two species appears to be related to the timing of their migration. Green sandpiper arrives two weeks earlier to its breeding grounds than the common sandpiper (Bird Life, 2021). This is very likely related to the fact that in the shallow waters of green sandpiper habitats, insect emergence starts earlier than in the larger and deeper lakes in which common sandpiper inhabit (Dessein-Lepasteur et al., unpubl., see also Orians and Wittenberger, 1991). Time can also be a limited resource because the peak of insect emergence at the beaver ponds might be short (Nummi, 1992). A delay in habitat selection thus can lead to fewer resources. The decision of habitat selection must be done early in the birds' arrival during spring migration to be reached early enough (Orians and Wittenberger, 1991), and it is probable that the green sandpiper arrives to its breeding landscape as early as possible in order to have time to detect the potential breeding sites. Beavers often flood new sites late summer, after green sandpipers have started their autumn migration, so in spring the flooded habitats might not be in the same places where the birds had experienced them to be (Nummi, pers. obs.). An additional advantage for the early arrival of green sandpipers is that vernal pools, another flooded habitat type they use, often dry early in the summer.

The stable habitats that common sandpiper preferred were larger lakes, whereas green sandpipers occupied smaller wetlands. Interestingly enough, the pattern of habitat use by common and green sandpiper bore a remarkable resemblance to what was found for common goldeneye *Bucephala clangula* and common teal in the very same landscape (Nummi et al., 2015). Common goldeneye's use of habitat was as stable as common sandpiper's, and that of the common teal was as variable as green sandpiper's found in this study. One thing in which the green sandpiper differs from the common teal, though, is that it is very territorial during brood rearing (Žďárek, 2004). For the common teal, several broods might inhabit even a relatively small wetland if it supports abundant food resources (pers. obs., see also Nummi et al., 2019a).

When studying the use of beaver sites by the green sandpiper, we noted that the number of green sandpipers was considerably higher at flooded beaver sites compared to the period before flooding. This pattern corresponded to those seen with the common teal (Nummi and Pöysä, 1997; Nummi and Hahtola, 2008). Common teal quickly inhabits newly inundated beaver habitats (Nummi and Pöysä, 1997), as we found for green sandpipers. Apart from benefitting from general increase of the production of invertebrates in flooded beaver habitats (Nummi and Hahtola, 2008), green sandpipers might use of freshly killed terrestrial invertebrates at the early stage of flooding (see Swanson et al., 1985; Nummi et al., 2021). One feature, not described for any waterbird species yet, is that the number of green sandpipers appeared to remain high also after flooding by beavers. It very likely is because even after the drawdown of the flood, the formerly flooded land remains moist and might contain small fishless puddles – a condition suitable for foraging by green sandpipers (Ormerod and Tyler, 1988; Žďárek, 2004). A higher abundance of songbirds has been observed in abandoned rather than active beaver ponds in Canada (Aznar and Desrochers, 2008). The beneficial habitat structure of beaver modified wetlands is further ameliorated by the high number of invertebrates found there (Nummi and Hahtola, 2008; Bush and Wissinger, 2016); the invertebrate production might continue at a higher level after flooding because of the organic matter deposited on the bottom of the beaver pond during flooding (Hodkinson, 1975; Dessborn et al., 2009; Nummi et al., 2018). The reason why the pattern was not clearer is that it takes place only in ponds surrounded by mires which have a low slope; the sandy shorelines dry relatively fast after flooding by beavers. The reason why common sandpiper did not make more use of beaver ponds very likely is that their shoreline often has too much higher vegetation; common sandpipers typically forage in rocky and shingle margins of water (Yalden, 1986). Also, Longcore

et al. (2006) did not find difference in the use of beaver ponds and glacial ponds by the spotted sandpiper *Actitis macularia* although they did for another wader, the common snipe *Gallinago gallinago*.

It appears that the beaver-created variability operates at a scale easily tracked by green sandpipers. In the use of the variable breeding habitat of the Evo study area, green sandpipers might use multimode movement strategies, as conceptually suggested by Riotte-Lambert and Matthiopoulos (2020). The birds might first use spatial memory to relocate predictable habitat features in a landscape, and thereafter establish a home range in that habitat feature. As noted earlier, beaver disturbance in a landscape is relatively predictable (Nummi and Kuuluvainen, 2013); therefore, in a beaver-influenced landscape, it is relatively easy for flying organisms to locate new patches, as has been discussed with the common teal (Nummi et al., 2019a). The fact that beaver sites are often clustered makes them even easier to be spotted by migratory birds (Kivinen et al., 2020).

Our findings concerning the green sandpiper adds to the growing literature demonstrating how engineering by beavers facilitates a myriad of organisms (Stringer and Gaywood, 2016), sometimes even whole species communities (Nummi and Holopainen, 2014; Romansic et al., 2020). From the point-of-view of enhancing natural wetland dynamics, facilitation by beaver is valuable. Of the European wetlands 60–90% were lost during the last century, and similar figures apply to many areas of North America as well (Junk et al., 2013); the losses have been larger and faster for inland than coastal natural wetlands (Davidson, 2014). Moreover, this decline and degradation of wetlands is known to negatively impact waterbirds depending on these habitats (Ma et al., 2010).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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