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Changing Landscapes and Declining Populations of Resident Waterbirds: A 12-Year Study in Bung Boraphet Wetland, Thailand

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Abstract

Changes in wetland environments can alter the dynamics of waterbird populations. We investigated the effects of hydrological and landscape variables on the abundance of resident waterbirds (ducks, fish-eaters, large waders, small waders, and vegetation gleaners) from 2003 to 2014 in Bung Boraphet, Thailand's largest freshwater wetland. Generalized linear mixed models were used to determine the effects of environmental variables on waterbird numbers, and generalized additive mixed models were used to identify the threshold for each effect. The results revealed that the population of all waterbirds declined by 27% from 2003 to 2014 with highest decline of 56% in ducks. Increasing water depth was negatively correlated with the abundance of small waders and vegetation gleaners. Higher concentrations of dissolved oxygen in the water increased the abundance of fish-eaters, while marshy areas were positively associated with the abundance of ducks, large waders, and vegetation gleaners. The abundance of fish-eaters, large waders, and small waders were negatively associated with the spatial area of waterbodies. Expanding human settlements decreased the abundance of vegetation gleaners, while vegetation infested by *Mimosa pigra* decreased the abundance of large waders. The study concludes that the maintenance of an optimal water depth and quality, preservation of critical marsh habitats, eradication of invasive species, and restrictions on new human settlements adjacent to wetlands are all necessary to conserve resident waterbird populations. Validating these findings in additional research sites is recommended before applying it to a broader landscape level.

Keywords

Bueng Boraphet, dissolved oxygen, feeding guilds, land-use, mixed modeling, resident waterbirds, waterbird conservation, water depth

Introduction

Waterbird populations are declining globally (Hansen, Menkhorst, Moloney, & Loyn, 2015; Z. Ma et al., 2014; W. Wang, Fraser, & Chen, 2017). The decline is particularly alarming in Asia where 50% of known populations were found to be in decline (Wetlands International, 2012). Waterbirds, an important component of wetland ecosystems, are sensitive to changes in the wetland environment; they either disperse or aggregate in response to such changes (Brandolin & Blendinger, 2016; Henry & Cumming, 2016). However, in some regions, the environmental variables affecting waterbird abundance are not yet clearly understood due to the complexity of the

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wetland environmental systems and differences in the composition and structure of avian communities.

Several studies have demonstrated that environmental variables such as wetland hydrology and landscape can alter waterbird abundance in different ways (Alexander & Hepp, 2014; Brandolin & Blendinger, 2016; Tavares, Guadagnin, de Moura, Siciliano, & Merico, 2015; Wen, Rogers, Saintilan, & Ling, 2011). For example, fluctuations in water depth influence the physical condition of waterbird habitats (e.g., the establishment of mudflats), affect food availability, and prey vulnerability (Bellio & Kingsford, 2013; Lantz, Gawlik, & Cook, 2011; Timmermans, Badzinski, & Ingram, 2008; Y. Wang et al., 2013; Zhang et al., 2016), which are characteristics that define habitat use by waterbirds (Jedlikowski, Chibowski, Karasek, & Brambilla, 2016). Likewise, the conversion of wetlands into agricultural areas and human settlements poses a significant threat to waterbirds. Other than direct habitat loss, such change in the wetland landscape also affects hydrological systems (Harrison & Whitehouse, 2012), and consequently, habitat use by the waterbirds (Cintra, 2015; Tavares et al., 2015). Therefore, understanding how different environmental variables affect waterbirds is important for the effective conservation of waterbirds and the management of their habitats. However, as different functional groups of waterbird respond differently to changes in environmental variables due to of varying habitat requirements, the relationship between waterbird abundance and environmental variables is complicated (Tavares et al., 2015). For instance, low concentrations of dissolved oxygen may affect waterbird species that use lake resources for foraging such as fish-eaters (Sulai et al., 2015), whereas similar changes may not affect species that use waterbodies solely as daytime roosts such as ducks. Some landscapes such as paddy fields may cause an increase in waterbird species that prefer shallow water for foraging (Acosta et al., 2010), but they are not a preferred habitat for the larger and more sensitive waterbird species like Black-headed Ibis *Threskiornis melanocephalus* (Sundar, 2006).

Bung Boraphet (BBP) in Central Thailand, a wetland of international importance proposed as a Ramsar site, provides an important habitat for both resident and migratory waterbirds (Office of Environmental Policy Planning, 2002). It is reported that BBP is under threat and increasing pressure due to hydrological and landscape changes such as water shortage, invasion of *Mimosa pigra*, and an increase in the area of land converted for agricultural use and human settlements (Chaichana & Choowaew, 2013; Sriwongsitanon, Surakit, & Hawkins, 2009). However, little research has been conducted on waterbirds and their environmental associations in BBP. There has been one study on the nest-site selection of a breeding visitor, Oriental Pratincole *Glareola maldivarum*, by Chaiyarat and Eiam-Ampai (2014), but no recent studies were found on resident waterbirds. Resident waterbirds might be at greater risk due to the rapidly changing local landscape and hydrology as they select a particular territory for a lifetime (West, Goss-Custard, dit Durell, & Stillman, 2005). Undesirable environmental changes reduce habitat availability (Orians & Wittenberger, 1991) and when such changes go beyond certain limits, they can lead to extinction of local populations (Peters & Otis, 2006). Therefore, a better understanding of the effects of changing hydrology and landscapes on the population trends and seasonal fluctuations of different functional groups of resident waterbirds would improve our in-depth knowledge of habitat use and enable the implementation of effective conservation measures.

This study was designed to investigate the effects of hydrological and landscape variables on waterbird abundance in BBP. To achieve this objective, we (a) assessed the long-term trends and seasonal variations in waterbird abundance in BBP from 2003 to 2014, (b) studied hydrological and land-use changes in BBP, and (c) examined the effect of hydrological and landscape variables on the abundance of resident waterbirds. Specifically, we tested the hypothesis that each of the five functional groups of resident waterbirds (ducks, fish-eaters, large waders, small waders, and vegetation gleaners) would show specific responses to changes in four hydrological variables (dissolved oxygen levels in the water, turbidity, water depth, and water temperature) and eight landscape variables (cover of fish farms, human settlements, landfills, marshes, mixed crops, paddy fields, vegetation infested by *Mimosa pigra*, and waterbodies). Finally, we proposed recommendations for the conservation of resident waterbirds and their habitats in BBP.

Methods

Study Site

This study was conducted in Bung Boraphet Wetland (BBP), Nakhon Sawan Province, Central Thailand (between latitude 15°40'N and 15°45'N and longitude 100°10'E and 100°23'E; Figure 1). BBP is the largest freshwater wetland on the floodplain of the Chao Phraya River, with a total area of approximately 212 km^2. It was developed in 1927 by the damming of a freshwater swamp to enhance fisheries (Sriwongsitanon et al., 2009). In 1937, this area was designated as a "Conservation Zone" to prevent human encroachment and settlement in the area. Nevertheless, by 2015, more than 32,000 people were living inside that zone (Department of Provincial Administration, 2015) and were making use of its natural resources such as fish and wetland vegetation. In addition, BBP has been used

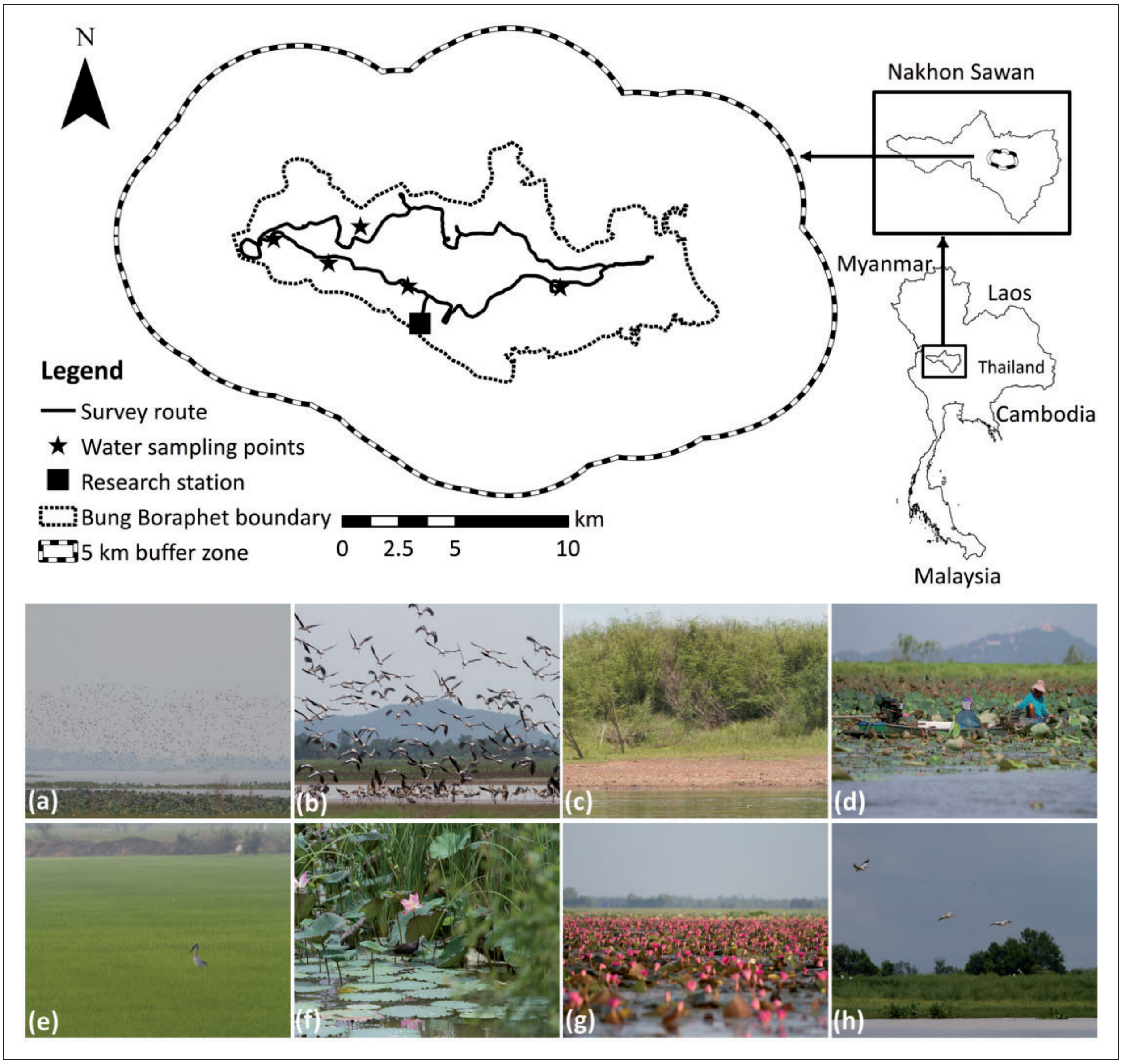


Figure 1. Location and map of the study area in Thailand. Five-kilometer buffer area surrounding the boundary of the lake, boat survey route used to count waterbird populations inside the lake, research station, and water sampling points are also shown. Photographs of the different waterbird species, wetland habitats, and threats/pressures in Bung Boraphet: (a) and (b) flocks of ducks and large waders; (c) vegetation dominated by *Mimosa pigra*; (d) fishermen harvesting wetland vegetation; and (e) to (h) waterbirds using different habitats (e.g., marshes and paddy fields). Photographs were taken by R. U. Haq.

for domestic and agricultural water supply and flood control. Incidents of direct waste disposal from the surrounding human settlements were also observed during the study period, which indicated that BBP was also used for waste disposal.

BBP supports a wide variety of flora and fauna because of its distinct geographical location, its variety of landscapes, and the natural dry–wet weather cycles (Jintanugool & Round, 1989). So far, 23 species of aquatic macrophytes including emerged, submerged, and floating aquatic plants, 93 species of phytoplankton, 43 species of zooplankton, and 77 species of fish have been recorded in BBP (Chaichana & Choowaew, 2013). Additionally, BBP is an important bird area (BirdLife International, 2017) that supports large numbers of resident and migratory waterbirds; around 36,000 and 20,060 waterbirds were counted in 1991 and 1994, respectively (Lopez & Mundkur, 1997). Although BBP is very important for wild flora and fauna, it has never been managed for wildlife conservation.

BBP lies in a tropical monsoonal climate zone. The wet season is from May to October, with around 78% of the annual rainfall occurring during this period. From 2003 to 2014, mean annual rainfall of 1,240 mm was recorded, while the monthly temperature varied during this period from an average minimum of 20.9 °C to an average maximum of 36.7 °C. According to the hydrological data from the Regional Environmental Office of Nakhon Sawan for the period of 2003 to 2014, the average water depth in BBP was 1.8 ± 0.7 m with a maximum water depth of 2.9 m recorded in 2011.

Waterbird Surveys

Count data for waterbirds were collected by Bung Boraphet Wildlife Research Station from January 2003 to December 2014. Boat surveys were conducted along a standardized route (Figure 1) starting from the research station at dawn. The surveys were conducted on a monthly basis in 2003 and 2004, and then once every 15 days from 2005 onwards. The time length of each survey was approximately 5 hours. There were slight changes in the survey route during the dry and wet seasons due to water depth differences, which restricted boat access to some areas. However, within each season, the survey route and time spent on each survey was consistent. Using binoculars, one pair of researchers searched for waterbirds on the right-hand side of the boat while another pair did the same on the left. Both teams coordinated their counts and shared information actively to avoid double counting. All waterbirds detected were recorded and identified into species. The seasonal status of all observed species (resident, migratory, or vagrant) was defined in accordance with the checklist of the Bird Conservation Society of Thailand (2016). Those species having both resident and migratory populations were classified as either resident or migratory depending on the predominant population (Philip Round, personal communication, January 26, 2017). Due to our focus on resident species, we did not consider migrants and vagrants in our analysis. We divided the resident waterbirds into broad functional groups based on their food preferences, following Kingsford's classifications (1991). Overall, five functional groups were recognized: ducks (all duck species), fish-eaters (e.g., cormorants, egrets, pelicans), large waders (e.g., ibises, spoonbills, storks), small waders (e.g., lapwings, plovers, stilts), and vegetation gleaners (e.g., jacanas, swamphens; Table 1).

Hydrological and Landscape Variables

We considered four hydrological variables (dissolved oxygen, turbidity, water depth, and water temperature) and area of eight landscape variables (fish farms, human settlements, landfills, marshes, mixed crops, paddy fields, vegetation, and waterbodies) as predictors. Hydrological data were obtained from the Regional Environmental Office, Nakhon Sawan Province. The team from Regional Environmental Office recorded the water depth in meters at five points inside BBP (Figure 1). From the same points, dissolved oxygen levels (mg/l) and water temperature (°C) were measured *in situ* using a multimeter and turbidity (NTU) was determined using a black and white Secchi disc (Figure 1).

Based on waterbirds' ecology and components of wetland habitat, the land-use of the landscape was classified into eight types: fish farms (fish farms and mixed aquaculture land), human settlements (built-up or developed

Table 1. Summary of the Functional Groups of Resident Waterbirds in Bung Boraphet Wetland.

Functional group	Typical species	Number of species studied	Annual mean abundance	CV
Ducks	Lesser Whistling-duck (*Dendrocygna javanica*), Cotton Pygmy-goose (*Nettapus coromandelianus*)	2	10,837	150.02
Fish-eaters	Little Cormorant (*Microcarbo niger*), Little Egret (*Egretta garzetta*), Oriental Darter (*Anhinga melanogaster*), Little Grebe (*Tachybaptus ruficollis*)	13	5,257	80.13
Large waders	Asian Openbill (*Anastomus oscitans*), Glossy Ibis (*Plegadis falcinellus*), Black-headed Ibis (*Threskiornis melanocephalus*)	3	6,959	132.43
Small waders	Black-winged Stilt (*Himantopus himantopus*), Red-wattled Lapwing (*Vanellus indicus*), Greater Painted-snipe (*Rostratula benghalensis*)	5	1,071	130.36
Vegetation gleaners	Pheasant-tailed Jacana (*Hydrophasianus chirurgus*), Purple Swamphen (*Porphyrio porphyrio*), Common Moorhen (*Gallinula chloropus*)	5	1,173	88.42

Note. CV = Coefficient of variation.

areas), landfills (places used to dispose of waste material by burying and covering it over with soil), marshes (marsh areas with emergent and floating wetland vegetation, e.g., sedges, reeds, lotus, water lilies, etc.), mixed crops (field crops other than rice, e.g., cassava, sugarcane, corn, watermelon, etc.), vegetation (grasslands, shrubs, and trees, including the invasive *Mimosa pigra*), paddy fields, and waterbodies (areas of open water without any wetland vegetation). These classifications were made using imagery from Landsat TM (for the year 2014) and land-use maps obtained from the Land Development Department, Thailand, for years 2001, 2007, 2009, and 2012. The Landsat imagery of 2014 was interpreted using Erdas Imagine 10 (Leica Geosystems, Atlanta, GA) by using supervised classification methods (visual interpretation techniques and ground surveys). To convert the raster data into vector data, ArcMap 10.2 (ESRI, Redlands, California, USA) was used. Since land-use changes around waterbody margins tend to affect waterbirds (Brown & Dinsmore, 1986) and may also affect aquatic habitat variables, we created a buffer of 5 km around the BBP boundary using the buffer tool in ArcMap 10.2. Due to the lack of yearly land-use data of BBP, we estimated the data for the missing years by fitting a linear regression; thus data for the missing years were derived from a fitted regression line. Explanatory variables are summarized in Table 2.

Statistical Analyses

To check the effect of predictor variables on waterbird abundance, we used generalized linear mixed models (GLMMs; Bolker et al., 2009) with a negative binomial distribution. Akaike's information criterion (AIC) was used for model selection (Burnham & Anderson, 2004); the best model is the one with the lowest AIC score. In some cases, where AIC scores for two models were not significantly different, we selected candidate models with cut-off criteria of $\Delta AIC<2$. Model averaging was used to evaluate the coefficients of uncertain models and unconditional standard errors. We used an 85% confidence interval to recognize variables with a significant effect on waterbirds: This interim reduces model choice and makes parameter-assessment criteria more harmonious than the smaller interim widths, for example, 95% (Arnold, 2010). We used the sum of the highest number of waterbirds recorded from monthly surveys as a response variable for each functional group for GLMMs. Predictor variables were added in the models in the following sequence: (a) influence of each variable; (b) all variables in a group, for example, all hydrological variables; and (c) hydrological and landscape variables together. The variable "year" was included in all models to account for possible correlation of observations among survey years. The data for waterbirds were overdispersed, and there was high variance in the counts between the wet and dry seasons due to the difference in survey routes between both seasons which affects the survey effort. Consequently, we treated season as a random effect (intercept) in all models to account for the nuisance parameter. We checked for outliers and collinearity before performing model fits following the recommendations of Zuur, Ieno, Walker, Saveliev, and Smith (2009). We applied Pearson's correlation test to all predictor variables. Highly correlated variables ($r > .5$) were not used in the same model. We standardized the data to dimensionless units (Z-scores) by subtracting the mean for each taxon and dividing this by its standard deviation in order to make resulting models directly comparable.

Table 2. Summary of Explanatory Variables.

Variable	Unit	Mean (range)
Water depth	m	1.81 (0.61–2.92)
Water temperature	°C	29.20 (12.31–34.00)
Turbidity	NTU	50.01 (4.40–407.01)
Dissolved oxygen	mg/l	5.70 (3.00–8.61)
Fish farms	ha	1,908.20 (1,537.11–2,343.91)
Human settlements	ha	3,550.01 (3,155.43–4,063.22)
Landfills	ha	13.76 (2.54–26.21)
Marshes	ha	9,878.20 (3,673.21–20,270.52)
Mixed crops	ha	5,563.47 (5,124.82–5,913.91)
Paddy fields	ha	16,318.79 (4,814.93–21,824.82)
Vegetation	ha	2,299.31 (1,191.71–2,759.14)
Waterbodies	ha	6,704.11 (3,820.31–7,404.32)

Note. NTU = Nephelometric turbidity unit; ha = hectares.

We assessed the appropriate level of each significant variable (obtained from GLMMs) graphically by consolidating smoothing capacities into the generalized additive mixed models (GAMMs) following Tavares et al. (2015). Different values of knots (k) were tested to make effective degrees of freedom (edf) not much less than $k-1$ for each model following the guidelines of Wood (2006).

Statistical analysis was performed in R (version 3.3.3). We used package glmmADMB (Skaug, Fournier, Nielsen, Magnusson, & Bolker, 2013) for GLMMs; wiqid (Meredith, 2016) for model selection; MuMIn (Barton, 2016) for model averaging; mgcv (Wood, 2006) for producing the response curves through GAMMs; and ggplot2 (Wickham, 2009) for creating plots.

Results

Waterbird Abundance and Species Composition

From 2003 to 2014, 35 species of resident waterbirds from 15 waterbird families were observed in BBP. Of these, 28 species (2 species of ducks, 13 species of fish-eaters, 3 species of large waders, 5 species of small waders, and 5 species of vegetation gleaners) were considered for further analysis based on the sufficiency of available records. The total population of the studied species changed every year with a mean value of 25,300 over a 12-year period.

Overall, resident waterbirds declined by 27% from 2003 to 2014. Ducks showed a long-term decline of 56%, particularly 56% for the Lesser Whistling-duck *Dendrocygna javanica* and 67% for Cotton Pygmy-goose *Nettapus coromandelianus*. Large waders declined by 25%, with the Asian Openbill *Anastomus oscitans* declining by 36%. Vegetation gleaners declined by approximately 8%. The populations of fish-eaters and small waders showed seasonal fluctuations, but overall populations of these functional groups remained stable throughout the study period. Moreover, there were clear wet–dry seasonal patterns for the ducks. The other four functional groups showed no regular seasonal patterns, although there appears to be a considerable year to year fluctuation (Figure 2).

Among the functional groups, ducks and large waders were the most dominant (60% of the total population). Among the families of waterbirds, Anatidae (ducks) were the most abundant, making up around 43.5% of the total waterbird population, followed by Ciconiidae (storks) accounting for 28%. The Lesser Whistling-duck *D. javanica* and the Asian Openbill *A. oscitans* were the predominant species, accounting for 39% and 26% of the total species, respectively. According to the categorizations of the IUCN Red List, we recorded one Vulnerable species—the Lesser Adjutant *Leptoptilos javanicus*—and five Near Threatened waterbird species—the Great Thick-knee *Esacus recurvirostris*, the Black-headed Ibis *Threskiornis melanocephalus*, the Oriental Darter *Anhinga melanogaster*, the River Lapwing *Vanellus duvaucelii*, and the Spot-billed Pelican *Pelecanus philippensis* (IUCN, 2017). The species observed within each functional group along with their annual mean abundance and global threat statuses are reported in Appendix A.

Hydrological and Land-Use Change

From 2003 to 2014, there were clear differences in water depth between seasons in which average water depth was higher during the wet seasons. Similarly, for the majority of the years, average turbidity and dissolved oxygen were higher during the wet seasons. No long-term decrease or increase was observed in the hydrological variables. On the other hand, some landscape variables showed considerable changes in the area. Land-use analysis showed that paddy fields were the most dominant landscape feature covering 47.2% of the total study area in 2014. In 2007, there was a significant decrease in the area of paddy fields due to an increase in marsh areas. The area accounted for by waterbodies declined by 31% from 2001 to 2014 (a major decline was observed after 2012 in the waterbody of BBP). The area of vegetation—dominated by *Mimosa pigra*—increased by 81% from 2001 to 2014. Both human settlements and fish farms showed an increase of 27% each. Marsh areas changed a little, except in 2007. After 2007, there was a decline till 2012. Also, there were changes in their distribution. The total areas accounted for by mixed crops and landfills exhibited minimal changes from 2001 to 2014. Land-use classification maps for the years 2001, 2007, 2009, 2012, and 2014 are shown in Figure 3. Seasonal variations and long-term trends in the hydrological and landscape variables from 2003 to 2014 are shown in Appendix B.

Effects of Hydrological and Landscape Variables on Waterbird Abundance

GLMMs suggested that increases in water depth decreased the abundance of small waders and vegetation gleaners. Increasing concentrations of dissolved oxygen showed a positive effect on the abundance of fish eaters. Among the landscape types, marshy areas were positively associated with the abundance of ducks, large waders, and vegetation gleaners, whereas the spatial area of waterbodies affected the abundance of fish-eaters, large waders, and small waders negatively. Vegetation area showed adverse effects on the abundance of large waders. Increases in human settlements had a negative effect on the abundance of vegetation gleaners. Although paddy fields appeared in one of our models, the effect was not statistically significant. Neither water temperature and turbidity nor areas of fish farms, mixed crops, and landfills exhibited any significant effect on any functional group of waterbirds. The negative binomial models revealed that hydrological and landscape variables had specific effects on different functional groups of waterbirds. The best GLMMs describing the abundance of waterbirds in BBP are shown in Table 3.

Average estimates of the coefficient of all variables present in the GLMMs revealed that two hydrological variables (dissolved oxygen and water depth) and four landscape variables (human settlements, marshes, vegetation, and waterbodies) were critical for resident waterbirds. The extent to which those variables affected waterbirds varied among different functional groups, as anticipated. Waterbirds showing long-term declines were mostly affected by the landscape variables, whereas the waterbird groups showing seasonal fluctuations were governed by the hydrological variables. Average estimates of the coefficient of the variables present in the most parsimonious GLMMs describing the abundance of waterbirds in BBP are shown in Table 4.

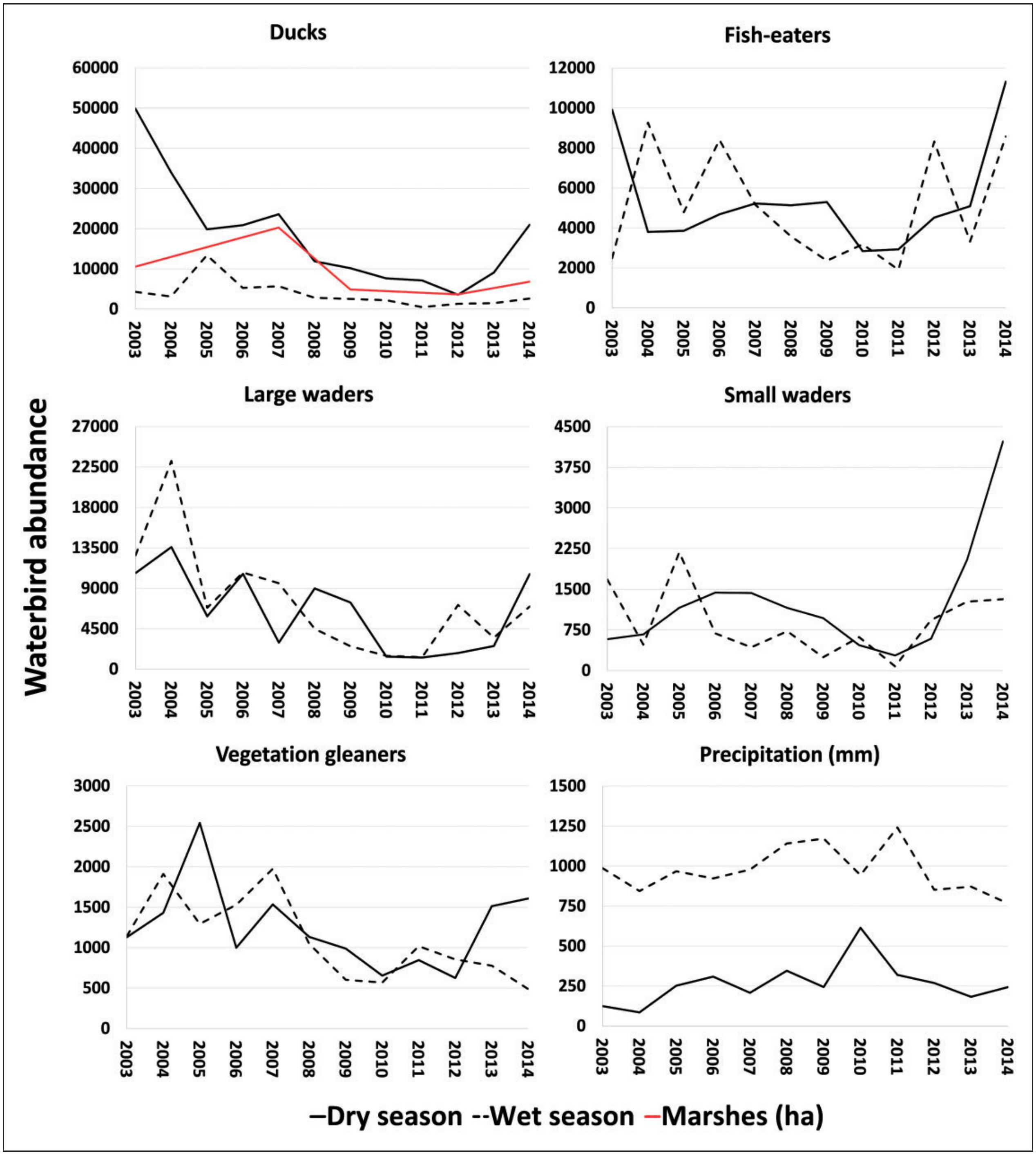


Figure 2. Annual mean waterbird abundance of five functional groups in Bung Boraphet Wetland during the dry and the wet season (2003–2014). Line chart showing precipitation (in millimeters) is shown. Line chart of "marsh area in hectares" is also shown indicating its association with the functional group ducks as they showed highest long-term declines.

GAMMs illustrated that fish-eaters were found in greater abundance when the level of dissolved oxygen in the water exceeded 5.5 mg/l. The appropriate water depth range for small waders and vegetation gleaners appeared to be less than 1.8 m; these waterbird groups showed a decrease in abundance after average water depths exceeded 1.8 m. Ducks, large waders, and vegetation gleaners showed a positive trend when marsh areas exceeded 6,500 ha, 6,700 ha, and 10,000 ha, respectively. Fish-eaters and large waders decreased in abundance after the spatial area of waterbodies exceeded 6,700 ha, while vegetation gleaners decreased in numbers when the area

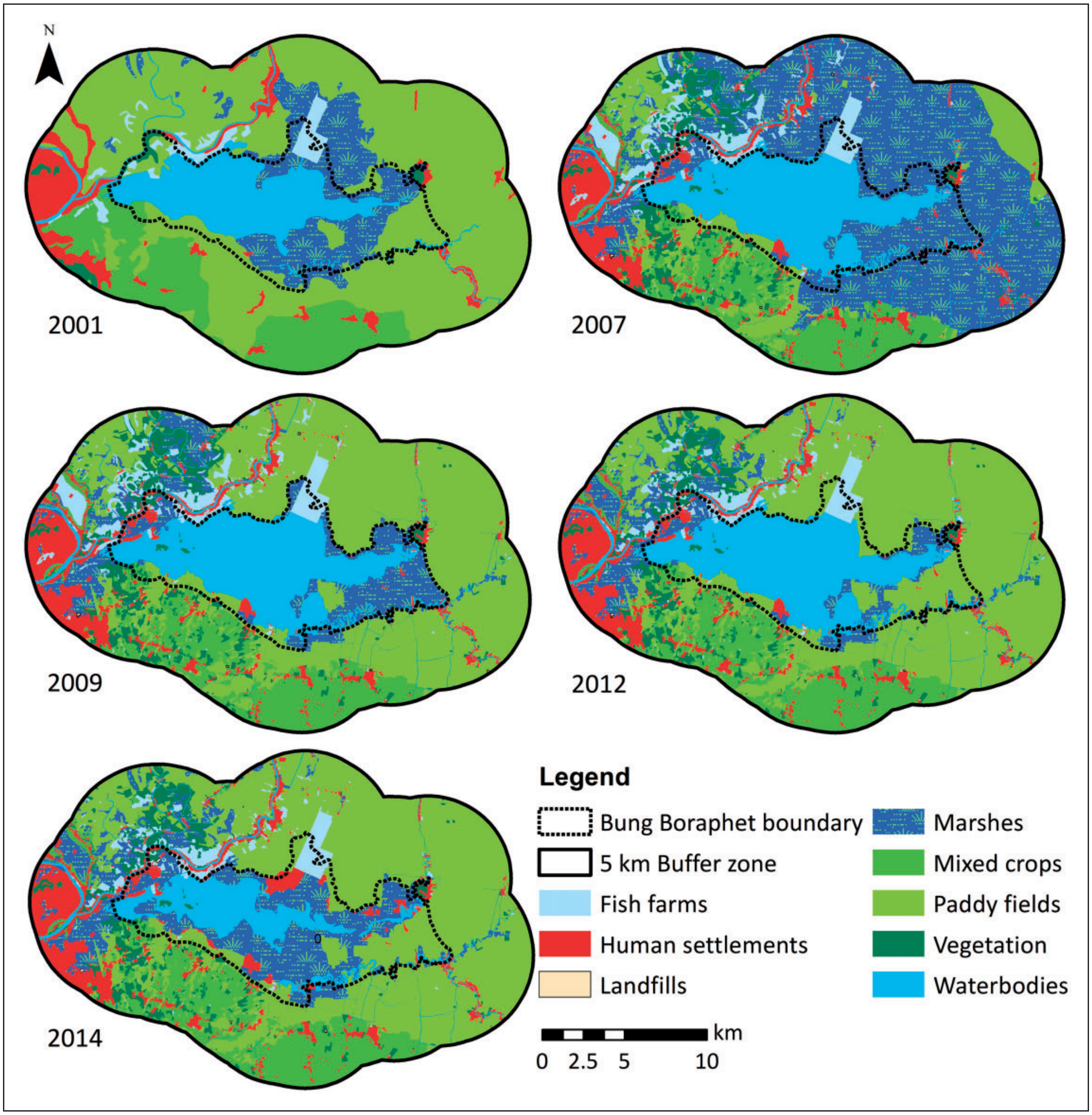


Figure 3. Land-use classification maps of the study area for Years 2001, 2007, 2009, 2012, and 2014.

of waterbodies exceeded 7,050 ha. Large waders decreased when the total vegetation area exceeded 2,300 ha. Vegetation gleaners also showed a decline in abundance when the area of human settlements around the lake exceeded 3,520 ha. Figure 4 illustrates response curves as function of the significant variables for each functional group.

Discussion

Our study detected a decline of 27% in the population of resident waterbirds from 2003 to 2014. Multiple studies have noted the declining numbers of waterbirds in Asia and Thailand (Mundkur, Langendoen, & Watkins, 2017; Wetlands International, 2010, 2012). The lowest abundance in overall waterbird population was observed in 2011, followed by a partial recovery from 2012 to 2014 (Figure 2). This trend could be due to a major flooding event in 2011 which overtopped the capacity of BBP. Waterbirds are likely to disperse as an immediate response to flooding; however, they return and reassemble on the main wetland area again as the flooded areas decline in extent (Poiani, 2006).

Table 3. List of the Best Generalized Linear Mixed Models (GLMMs) Explaining the Abundance of Resident Waterbirds in Bung Boraphet Wetland.

Functional groups of resident waterbirds	K	AIC	Δ AIC	*w*
Ducks (17 models tested)				
Marshes	4	2,844.16	0.00	0.99
Null model	3	2,872.96	28.80	0.00
Fish-eaters (18 models tested)				
Dissolved oxygen + waterbodies	5	2,656.16	0.00	1.00
Null model	3	2,704.84	48.70	0.00
Large waders (26 models tested)				
Waterbodies + vegetation + marshes	6	2,785.14	0.00	0.51
Waterbodies + vegetation + paddy fields	6	2,785.28	0.14	0.48
Null model	3	2,818.00	32.92	0.00
Small waders (16 models tested)				
Water depth + waterbodies	5	2,237.74	0.00	0.99
Null model	3	2,275.94	38.20	0.00
Vegetation gleaners (21 models tested)				
Water depth + marshes	5	2,247.76	0.00	0.60
Water depth + marshes + human settlements	6	2,249.32	1.56	0.28
Null model	3	2,274.16	26.40	0.00

Note. K = Number of parameters estimates + intercept; AIC = Akaike's Information Criterion; Δ AIC = Difference in AIC score between ranked models; *w* = Model weight. Predictor variables occurring in the model sets are as follows: (a) marshes (marsh areas in hectares with emergent and floating wetland vegetation), (b) vegetation (natural vegetation in hectares including grasslands, shrubs, trees, and the invasive *Mimosa pigra*), (c) waterbodies (areas of open water in hectares without any vegetation), (d) human settlements (built-up or developed areas in hectares), (e) paddy fields (rice fields in hectares), (f) dissolved oxygen levels (mg/l), and (g) water depth in meters (m).

Table 4. Average Estimates of the Coefficients, Unconditional Standard Errors, and Confidence Intervals of the Variables Present in the Best Generalized Linear Mixed Models (GLMMs).

Functional groups of resident waterbirds or predictors	Estimate	Uncond. *SE*	Lower 85%	Upper 85%
Ducks				
Marshes	0.56	0.10	0.42	0.70
Fish-eaters				
Dissolved oxygen	0.32	0.05	0.25	0.40
Waterbodies	−0.20	0.05	−0.26	−0.13
Large waders				
Marshes	0.39	0.09	0.26	0.53
Vegetation	−0.30	0.09	−0.44	−0.17
Waterbodies	−0.21	0.10	−0.35	−0.07
Paddy fields	−0.03	0.09	−0.05	0.02
Small waders				
Water depth	−0.41	0.09	−0.54	−0.28
Waterbodies	−0.37	0.09	−0.51	−0.23
Vegetation gleaners				
Marshes	0.28	0.05	0.20	0.36
Water depth	−0.12	0.06	−0.20	−0.05
Human settlements	−0.05	0.06	−0.12	−0.01

Note. Uncond. *SE* = Unconditional standard error. Predictor variables occurring in the model sets are as follows: (a) marshes (marsh areas in hectares with emergent and floating wetland vegetation), (b) vegetation (natural vegetation in hectares including grasslands, shrubs, trees, and the invasive *Mimosa pigra*), (c) waterbodies (areas of open water in hectares without any vegetation), (d) human settlements (built-up/developed areas in hectares), (e) paddy fields (rice fields in hectares), (f) dissolved oxygen levels (mg/l), and (g) water depth in meters (m).

A long-term decline was observed in the populations of *D. javanica* and *N. coromandelianus*. The fifth edition of the waterbird population estimates (Wetlands International, 2012) reported a decreasing trend in the population of *D. javanica* and an unknown population status of *N. coromandelianus* in Asia. The coordinated counts of waterbirds in Asia and Australasia showed a decline of 24% in the population of *D. javanica* from 2008 to 2015 in Asia, but no change was observed in the population of *N. coromandelianus* (Mundkur et al., 2017). However, as the survey numbers fluctuated wildly from year to year between 2008 and 2015, the uncertainty across the population trends for this report is significant. Therefore, in the present study, we hypothesize that the decline in the population of ducks is associated with the changes in marsh area (Figure 2). The 25% decline in the population of large waders (primarily *A. oscitans*) was due to the outbreak of avian flu in 2004, which wiped out breeding colonies (Siengsanan et al., 2009; Suksatu et al., 2009). The birds that recovered from this outbreak were subsequently affected by extensive flooding in 2011, which may have either caused a population crash or reduced the availability of their principal prey Applesnail *Pomacea canaliculata* (Philip Round, personal communication, April 25, 2017).

Nevertheless, ducks and large waders were the dominant functional groups as BBP still offers an excellent roosting site for ducks, while the surrounding paddy fields also act as feeding grounds for ducks and large waders (Chaiyarat, Sookjam, Eiam-Ampai, & Damrongphol, 2015). For the smaller and less conspicuous species of waterbirds (e.g., small waders and vegetation gleaners), detectability differences might play a major role, particularly during the rainy season. In addition, dense wetland vegetation preferred by vegetation gleaners might also reduce their detectability.

The land-use analysis suggested that there were significant changes in the areas of waterbodies, vegetation, human settlements, and fish farms from 2001 to 2014. The total area of the waterbodies showed a decline of 31% from 2001 to 2014. Classified land-use maps

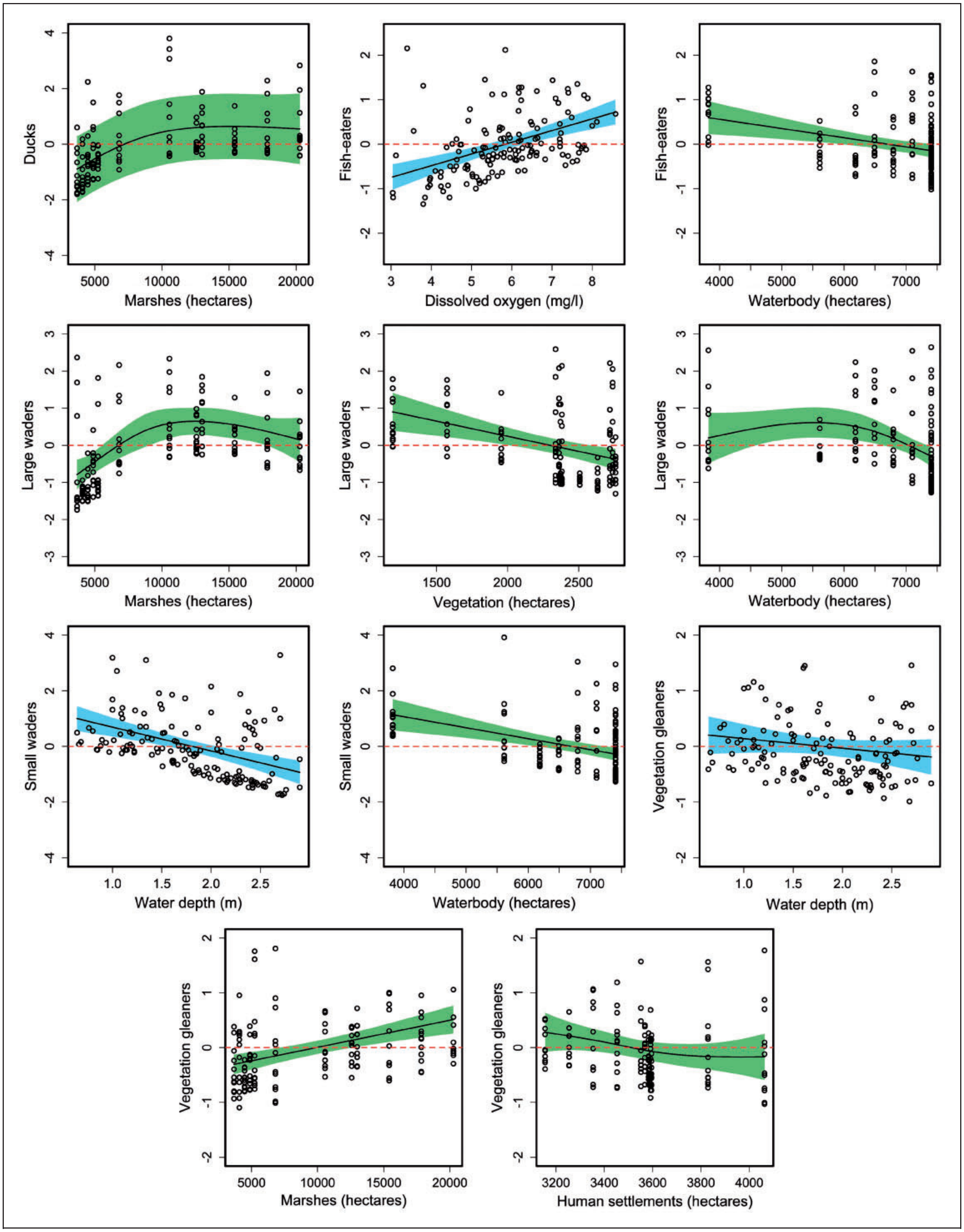


Figure 4. Waterbird abundance responses to significant variables obtained using generalized additive mixed models. Shaded areas show 95% while circles indicate partial residuals. Blue-shaded graphs indicate hydrological variables, and green-shaded graphs indicate landscape variables.

showed a conversion of some waterbodies into human settlements and paddy fields (Figure 3). Rapidly expanding human settlements, unsustainable land-use practices (Chaichana & Choowaew, 2013; Sriwongsitanon, Surakit, Hawkins, & Chandrasena, 2007), and unregulated pumping of water from BBP for the cultivation of dry-season rice (Sriwongsitanon et al., 2009) were likely the main reasons for this decrease. The rapid increase in vegetation cover was due to the invasion of *Mimosa pigra*. In suitable habitats, where water aids seed dispersal, mimosa can out-compete local vegetation (Rijal & Cochard, 2016). Significant changes in the marsh area and paddy fields were observed in 2007. These changes were caused by two small flooding events, which transformed the paddy fields into marsh areas due to water retention. In addition, there were changes in the distribution of the marshy areas due to the shrinkage of the total waterbody area of BBP and the expansion of the paddy fields. The long-term trends and seasonal variations in the waterbird populations, decline in area of some landscape variables, and fluctuations in hydrological variables between dry and wet season appear to indicate that both hydrological and landscape variables are affecting waterbirds in BBP.

GLMMs results suggested that the assemblage of each functional group of waterbirds was influenced by a distinct set of hydrological and landscape variables. Groups of waterbirds showing seasonal fluctuations but a stable population (i.e., fish-eaters and small waders) were governed by seasonally fluctuating hydrological variables, while groups showing long-term trends (i.e., ducks, large waders, and vegetation gleaners) were governed by the changes in landscape variables. Increases in water depth caused the abundance of small waders and vegetation gleaners to decrease. Appropriate level of water is very important as it dictates the feeding success for small waders (Lantz et al., 2011) and vegetation gleaners (Zhang et al., 2016). Small waders usually prefer shallow waters because their small bills restrict the catching of prey beyond a certain water depth (Lantz, Gawlik, & Cook, 2010). Shallow waters also favor macrophyte growth (Zhang et al., 2016), which serves as a nesting and feeding habitat for vegetation gleaners, such as moorhens (*Gallinula chloropus*; Forman & Brain, 2004). Dissolved oxygen levels were positively associated with the abundance of fish-eaters. Sulai et al. (2015) observed a similar relationship between tropical waterbird species and dissolved oxygen levels in Peninsular Malaysia. Fish is the main food resource for fish-eaters, and sufficient concentrations of dissolved oxygen enhance fish survival (Williams et al., 2004). Greater availability of feeding resources and higher levels of dissolved oxygen were the reasons for this positive association.

Among the landscape variables, increase in the marsh area was positively associated with the abundance of ducks, large waders, and vegetation gleaners. MacDonald and Henderson (1977) explained that marshes attract more waterbird species compared with other landscapes (e.g., open water) by offering more shelter, an abundance of food, suitable nesting, and safe roosting sites. Ali, Ripley, and Dick (1987) and Upadhyaya and Saikia (2010) in their respective studies of the Cotton Pygmy-goose *N. coromandelianus* and the Lesser Whistling-duck *D. javanica* observed that both species prefer marshes compared with other habitats. In contrast to marsh areas, open water areas have higher predation risk and less food (Kleijn, Cherkaoui, Goedhart, van der Hout, & Lammertsma, 2014). As a result, increases in the spatial area of waterbodies showed negative effects on the abundance of fish-eaters, large waders, and small waders in this study. Changes in vegetation areas showed a negative effect on large waders. It is apparent that the invasion of *Mimosa pigra* has changed the vegetation structure so that it is no longer suitable for large waders. *Mimosa pigra* can transform tropical wetlands into monospecific stands that no longer support local birds and vegetation (Braithwaite, Lonsdale, & Estbergs, 1989). Moreover, waterbirds mostly rely on visual cues to detect prey, and complex vegetation may reduce prey accessibility and detectability (Pérez-García, Sebastián-González, Alexander, Sánchez-Zapata, & Botella, 2014). For example, the *A. oscitans* feeds majorly on the Applesnail *P. canaliculata* (Sawangproh, Round, & Poonswad, 2012), and vegetation reduces Applesnail's detectability by providing it with more hiding spaces (Meyer-Willerer & Santos-Soto, 2006). Human settlements showed negative effects on vegetation gleaners. Habitat degradation and competition between waterbirds and humans for the same resources are the likely reasons for this negative association. For example, water lilies provide excellent foraging and nesting habitat for vegetation gleaners. However, people around BBP also use and harvest water lilies as a food resource (Chaichana & Choowaew, 2013). The expansion of human settlements and increasing human populations inside the conservation zone of BBP are likely causing an increase in the harvesting of such resources, thus affecting vegetation gleaners.

Some important landscape variables, for example, fish farms and paddy fields, exhibited no significant effect on waterbird abundance in this study. However, studies from other regions have shown that paddy fields (Fasola, Canova, & Saino, 1996; Z. Ma, Cai, Li, & Chen, 2010) and fish farms (Feaga, Vilella, Kaminski, & Davis, 2015; Rocha, Ramos, Paredes, & Masero, 2017) can provide alternative habitats for waterbirds. We, therefore, call for further in-depth investigations so as to understand the relationships between the waterbird abundance and these variables with greater certainty.

More specifically, a detailed study is needed to understand the effects of the invasive *Mimosa pigra* on waterbirds and wetland habitats in BBP.

In summary, our results support the proposed hypothesis that the effects of hydrological and landscape variables are specific to different functional groups of waterbirds. A strong association was observed between waterbird groups showing long-term declines (ducks, large waders, and vegetation gleaners) and landscape variables (marshes, waterbody, vegetation infested by *Mimosa pigra*, and human settlements), and an association was observed between waterbird groups showing stable populations (fish-eaters and small waders) and hydrological variables (water depth and dissolved oxygen). Water depth, dissolved oxygen levels, marshy areas, vegetation, waterbodies, and human settlements were critical variables for resident waterbirds in BBP.

Implications for Conservation

The study suggests that management should focus on both hydrological and landscape variables when implementing waterbird conservation and habitat restoration in freshwater wetlands. Our results also indicate that each functional group of waterbirds has its own specific hydrological and landscape needs; as a result, management efforts to conserve freshwater wetland habitats should be specific for different functional groups of waterbirds.

Among the hydrological variables, the average water depth of BBP should be maintained at a level of 1.8 m for supporting populations of small waders and vegetation gleaners. Levels of dissolved oxygen in the water should be maintained at a minimum of 5.5 mg/l to support food resources for fish-eaters. This operation can be jointly implemented by restoring the total area of the waterbodies—which was 3,820 ha in 2014—to a maximum of 6,500 ha, as above this size, the total area of waterbodies is shown to have negative effects on waterbird species. Providing this area of waterbodies will not only help to maintain water depth but will also maintain dissolved oxygen levels due to the greater surface area of the water. Regulating the water usage of rice farmers around BBP during the dry season can help to maintain the waterbody area in BBP (Sriwongsitanon et al., 2009). Maintaining an appropriate spatial area of waterbodies could also help to maintain a suitable area of marshes. Management should seek to maintain marsh areas at 6,500 ha, 6,700 ha, and 10,000 ha for ducks, large waders, and vegetation gleaners, respectively. The invasive weed *Mimosa pigra* should be eliminated by the regular pulling of young sprouts and the cutting of mature plants before flooding. The resprouting ability of mimosa significantly decreases underwater, leading to its death (Son et al., 2004). To reduce the resource competition between waterbirds and humans, there is a dire need to explore livelihood strategies and the factors causing an increase in human population inside the conservation zone. Furthermore, livelihood practices, which are in conflict with the waterbird conservation, need to be replaced with those practices that can benefit both people and wildlife. For example, enhancement of the habitat value of paddy fields for waterbirds in California's Central Valley has resulted in great benefits for the farmers and improved habitat to support the waterbirds (California Rice Commission, 2014). Similarly, restricting the use of pesticides and herbicides, decreasing the application of chemical fertilizers, using efficient irrigation processes, and providing economic incentives to the rice farmers who could maintain shallow waters in abandoned rice fields could provide alternative habitat for some waterbird groups. Most importantly, a proper protection status along with law enforcement is urgently required if BBP is to continue to sustain its diverse resident and migratory avifauna.

This study represents the most comprehensive assessment of waterbirds and their environmental associations yet conducted for any wetland in Southeast Asia. In general, this study will not only fill the information gap on waterbird populations in BBP and Thailand but will also contribute to waterbird conservation in Southeast Asia and along the East Asian-Australasian Flyway because waterbird populations are significantly declining in this region and quality information is lacking (Mundkur et al., 2017). Meanwhile, the quantitative approach used in this study would be of use in supporting authorities to evaluate waterbird-environment associations and to undertake strategies for effective conservation.

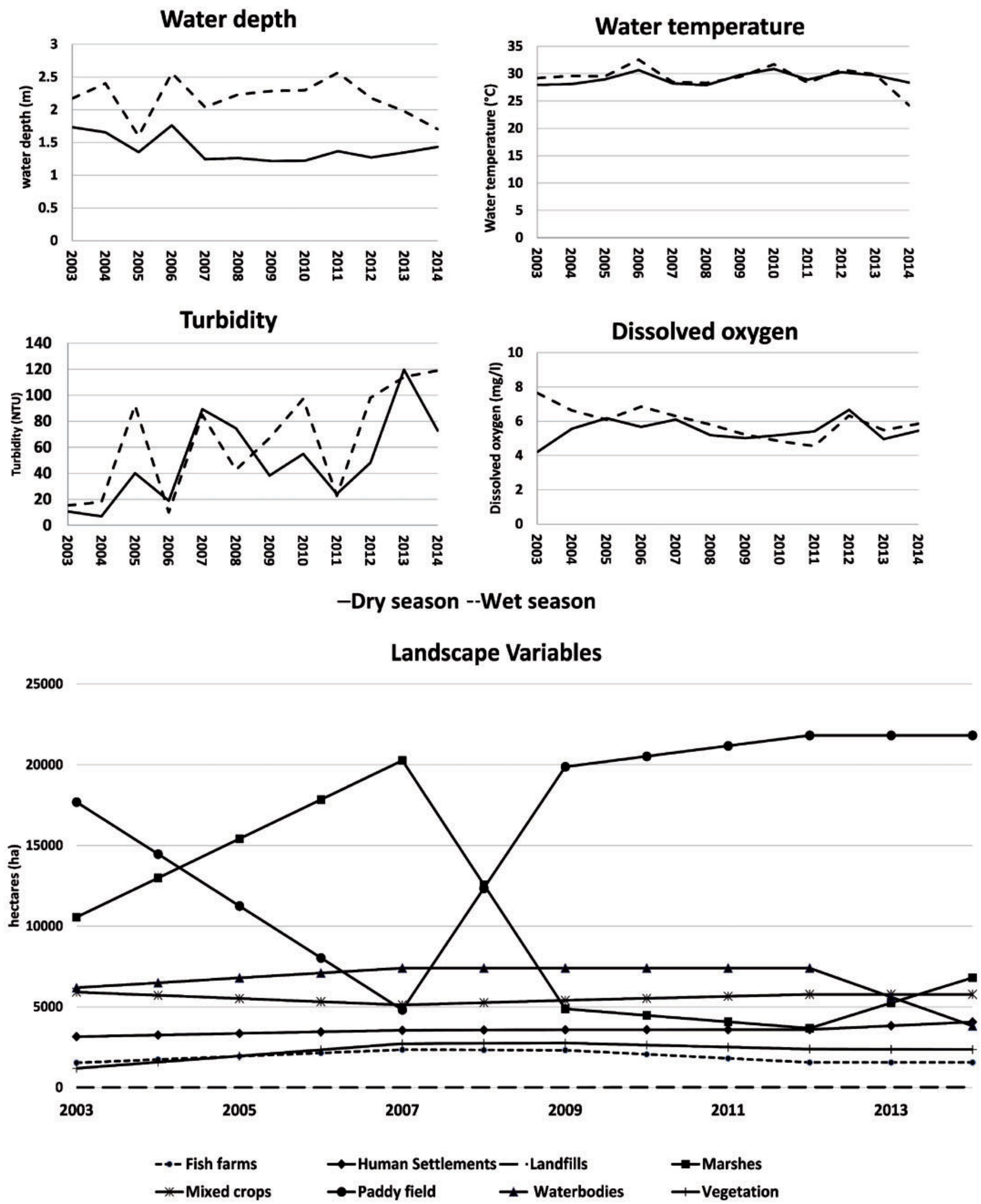
Appendix A. Annual Mean Abundance of Resident Waterbird Species Detected in the Bung Boraphet Wetland, Thailand.

Functional group	Family	Common name	Scientific name	GTS	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014
Duck	**Anatidae**	**African Comb Duck**	***Sarkidiornis melanotos***	**LC**	0	0	0	2	0	1	3	0	1	0	0	1
	Anatidae	Cotton Pygmy-goose	*Nettapus coromandelianus*	LC	1,321	775	1,751	495	273	475	752	888	312	124	228	438
	Anatidae	**Indian Spot-billed Duck**	***Anas poecilorhyncha***	**LC**	0	0	0	0	0	0	0	0	0	1	0	2
	Anatidae	Lesser Whistling-duck	*Dendrocygna javanica*	LC	25,763	16,392	14,870	12,573	14,367	6,886	5,603	4,042	3,499	2,330	5,066	11,355
Fish-eater	Anhingidae	Oriental Darter	*Anhinga melanogaster*	NT	54	4	8	10	33	103	81	49	71	85	60	166
	Ardeidae	Black-crowned Night-heron	*Nycticorax nycticorax*	LC	0	0	183	1,101	433	253	137	135	203	161	235	405
	Ardeidae	Cattle Egret	*Bubulcus ibis*	LC	453	1,194	373	1,362	1,002	435	284	121	62	210	205	1,249
	Ardeidae	Cinnamon Bittern	*Ixobrychus cinnamomeus*	LC	13	9	3	6	16	15	12	3	6	4	3	10
	Ardeidae	Great White Egret	*Ardea alba*	LC	590	245	316	217	193	240	166	188	162	800	391	747
	Ardeidae	Intermediate Egret	*Ardea intermedia*	LC	758	95	105	107	160	70	129	115	123	240	143	711
	Ardeidae	**Javan Pond-heron**	***Ardeola speciosa***	**LC**	3	0	0	0	0	0	0	1	0	1	1	0
	Ardeidae	Little Egret	*Egretta garzetta*	LC	580	2,113	964	2,178	1,693	1,462	1,258	561	330	2,064	1,194	2,829
	Ardeidae	Purple Heron	*Ardea purpurea*	LC	121	538	117	143	101	64	47	76	90	103	105	158
	Ardeidae	Yellow Bittern	*Ixobrychus sinensis*	LC	16	13	6	8	18	24	20	22	17	11	17	52
	Pelecanidae	Spot-billed Pelican	*Pelecanus philippensis*	NT	6	17	24	20	38	41	21	25	4	54	29	33
	Phalacrocoracidae	Indian Cormorant	*Phalacrocorax fuscicollis*	LC	0	0	0	6	13	50	65	83	206	1,067	609	1,713
	Phalacrocoracidae	Little Cormorant	*Microcarbo niger*	LC	820	1,958	1,158	991	988	1,094	940	842	947	1,359	1,123	1,681
	Podicipedidae	Little Grebe	*Tachybaptus ruficollis*	LC	2,786	596	1,065	395	505	503	670	791	200	266	89	191
Large wader	Ciconiidae	Asian Openbill	*Anastomus oscitans*	LC	11,678	18,803	6,341	10,660	6,231	6,673	4,913	1,344	1,278	4,384	2,982	8,540
	Ciconiidae	**Lesser Adjutant**	***Leptoptilos javanicus***	**VU**	0	0	0	1	0	0	0	0	0	0	0	0
	Threskiornithidae	Black-headed Ibis	*Threskiornis melanocephalus*	NT	2	1	3	0	1	5	1	5	1	3	2	9
	Threskiornithidae	Glossy Ibis	*Plegadis falcinellus*	LC	2	11	8	15	23	57	68	86	27	74	53	220
Small waders	**Burhinidae**	**Great Thick-knee**	***Esacus recurvirostris***	**NT**	0[a]	0	0	0	0	0	0	0	0	0	0	0
	Burhinidae	**Indian Thick-knee**	***Burhinus indicus***	**LC**	0[a]	0	0	0	0	0	0	0	0	0	0	0
	Charadriidae	Little Ringed Plover	*Charadrius dubius*	LC	35	14	23	26	81	46	58	17	5	18	42	84
	Charadriidae	Red-wattled Lapwing	*Vanellus indicus*	LC	69	61	46	53	99	115	76	16	24	78	53	188
	Charadriidae	**River Lapwing**	***Vanellus duvaucelii***	**NT**	1	0	0	0	0	0	0	0	0	0	0	0
	Glareolidae	Small Pratincole	*Glareola lactea*	LC	33	45	74	65	11	23	29	19	1	7	157	109
	Recurvirostridae	Black-winged Stilt	*Himantopus himantopus*	LC	965	418	1,523	917	727	754	442	493	145	655	1,402	2,389
	Rostratulidae	Greater Painted-snipe	*Rostratula benghalensis*	LC	29	26	4	2	13	4	2	0	4	3	2	3
Vegetation gleaners	Jacanidae	Bronze-winged Jacana	*Metopidius indicus*	LC	88	99	45	66	46	48	26	11	33	22	28	37
	Jacanidae	Pheasant-tailed Jacana	*Hydrophasianus chirurgus*	LC	305	739	404	292	306	327	219	232	186	206	229	307
	Rallidae	Common Moorhen	*Gallinula chloropus*	LC	18	41	57	36	20	24	22	18	17	19	32	89
	Rallidae	Purple Swamphen	*Porphyrio porphyrio*	LC	692	786	1,400	858	1,377	679	520	347	691	487	850	604
	Rallidae	White-breasted Waterhen	*Amaurornis phoenicurus*	LC	31	29	12	14	7	12	8	3	5	6	6	10

Note. GTS = Global Threat Status according to IUNC Red List criteria (LC: Least Concern; NT: Near Threatened; VU: Vulnerable; IUCN, 2017-2). The waterbird species in bold were not considered for GLMMs and GAMMs due to fewer records.

[a]For Great Thick-knee *Esacus recurvirostris* only two individuals and for Indian Thick-knee *Burhinus indicus* only five individuals were sighted in 2003.

Appendix B. Line charts showing trends in hydrological and landscape variables tested over 12-year study period (2003–2014).



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