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Effects of seasonal hydrological connectivity on Eurasian Spoonbill *Platalea leucorodia* foraging ecology

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Abstract Seasonal inundation is a key aspect of flood pulse ecosystems, connecting otherwise isolated river channels and lakes into a panmictic floodplain. This period of hydrological connectivity is strongly linked with biological productivity. Particularly in systems that serve as winter refuge for migratory wildlife, time-lags exist between the increase of habitat productivity at lower trophic levels and increases in foraging at higher trophic levels. These time-lags make it difficult to assess the ecological importance of flooding solely through within-season observations. We examine the effects of hydrological connectivity on waterbird habitat selection to quantify the ecological impact of summer flooding on conditions during the following winter. We calculated the number of days in which summer overbank flow connected Sha Hu and Bang Hu sub-lakes of Poyang Lake (China) and then constructed a series of regression models comparing the area of preferred winter foraging habitat of Eurasian Spoonbill *Platalea leucorodia* with spoonbill use days under three different flooding conditions: years with above-average, average, and below-average duration of hydrological connectivity. In both the average and below-average inundation conditions, spoonbill use days were positively correlated with extent of preferred habitat, suggesting that spoonbills typically rely on these habitats for foraging. However, in years with greater hydrological connectivity, extent of preferred habitat and spoonbill use days were not related. Seasonal flood pulses play an important role in structuring Eurasian Spoonbill foraging behavior and the duration of connectivity in summer alters habitat use in winter.

Keywords Eurasian Spoonbill, *Platalea leucorodia*, flood pulse ecology, foraging habitat, habitat use, Poyang Lake, wintering ecology.

Introduction

Natural flow or pulse regimes are key drivers of productivity in floodplain wetland ecosystems (Bunn and Arthington 2002), and hydrological variability is particularly important for waterbird communities (Kingsford *et al.* 2004). Seasonal floods trigger productivity at a variety of trophic

levels: inundation has a major role in nutrient cycling and brings inflows of organic carbon and other nutrients (Sparks 1995; Thoms 2003), leads to an increase in plant and invertebrate biomass (Anderson and Smith 2000; Sheldon *et al.* 2002; Jenkins and Boulton 2003), provides a vector for larger aquatic biota to re-colonize seasonally inhabited areas (Poff and Allan 1995), and, by increasing system-wide productivity, results in a higher abundance of predators that rely on these lower trophic levels (Kingsford *et al.* 2004).

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Floods such as overbank flows create hydrological connectivity, a key facet of flood pulse systems (Bunn and Arthington 2002) and of vital importance for waterbirds (Guadagnin and Maltchik 2007). In a connected basin, aquatic organisms may freely move throughout the entire floodplain system during the inundation phase. Within Poyang Lake, drawdowns in autumn and winter follow high water periods in summer (Shankman *et al.* 2006). During drawdowns, the receding water concentrates and eventually traps organisms in sub-basins, creating patches of high biomass throughout the wetland matrix (Beerens *et al.* 2011; Lorenz 2014). Migratory waterbirds arrive in winter during or after the drawdown period and utilize these areas of concentrated food items (Li *et al.* 2012).

Anthropogenic disturbance and regulation of natural flow regimes tend to degrade flood pulse ecosystems (Arthington and Pusey 2003; Kingsford and Thomas 2004). For example, upstream dam construction reduces or halts sediment flow, increases the difficulty of migration for aquatic biota, and reduces water minima and maxima (Kingsford and Thomas 2004; Guo *et al.* 2012). In ecosystems worldwide, disrupted natural flow regimes have consistently and dramatically reduced fish abundance (Naiman *et al.* 2002; Bunn and Arthington 2002) and eroded biodiversity (Brinson and Malvarez 2002; Tockner and Stanford 2002). These changes may be even more pronounced for waterbirds: artificial water level stabilization triggered an 80% or greater decline in waterbird abundance across all functional groups in Australia's Murray-Darling flood pulse ecosystem (Kingsford and Thomas 2004) and similar changes have occurred in the Yangtze system at Shengjin Lake (Fox *et al.* 2011).

Poyang Lake is at risk of hydrological disruption from extensive sand dredging (de Leeuw *et al.* 2010; Lai *et al.* 2014a) and potential construction of an outlet dam at Hukou (Wang *et al.* 2013). The Three Gorges Dam, nearly 1,000 km upstream, has been shown to significantly impact the middle-lower Yangtze River (Zhang *et al.* 2015), reducing variability and decreasing the annual mean water level (Lai *et al.* 2014b). Understanding the role of hydrological

fluctuations in determining the food abundance and availability is the first step in mitigation of these effects.

This study assesses how summer flooding affects winter waterbird habitat use in Poyang Lake. In particular, we examine whether the duration of summer inundation (the period of connectivity) changes the relationship between Eurasian Spoonbill *Platalea leucorodia* abundance and extent of preferred spoonbill winter habitat. By quantifying the connectivity between a perennially productive sub-lake and the greater Poyang wetland complex, we categorize and compare annual hydrological conditions in relation to Eurasian Spoonbill habitat use. We hypothesize that 1) years with reduced summer connectivity will result in lower winter spoonbill densities and decreased use of suitable foraging habitat, indicating poorer foraging conditions; 2) years with typical connectivity will result in average densities and average use of suitable foraging habitat; and 3) years with greater connectivity will result in greater densities and decreased use of suitable foraging habitat due to increased prey abundance and superior foraging conditions.

Study area

During the summer wet season, Poyang Lake is the largest freshwater lake in China (Shankman *et al.* 2006) and provides critical wintering habitat for migratory waterbirds along the East Asian – Australasian Flyway (Barter *et al.* 2005; Wang *et al.* 2013). Poyang Lake serves both as a floodplain for the Yangtze River to the north and for five tributary rivers to the south. Flood pulses from these rivers seasonally inundate Poyang Lake as widespread overbank flows provide basin-wide hydrological connectivity (Shankman and Liang 2003; Wu *et al.* 2009). During the summer flood months, Poyang's surface area can increase to as large as 3,000 km² (Feng *et al.* 2013). During the autumn drawdown period, water is concentrated in smaller sub-basins such as those within the boundaries of Poyang Lake National Nature Reserve (PLNR). Within PLNR, Sha Hu sub-lake (N 29° 10', E 115° 56'; Figure 1) serves as wintering habitat for wading birds including the Eurasian Spoonbill and the endangered Oriental White Stork *Ciconia boyciana* (Zeng *et al.* 2012).

Methods

Four analyses were performed with hydrological and



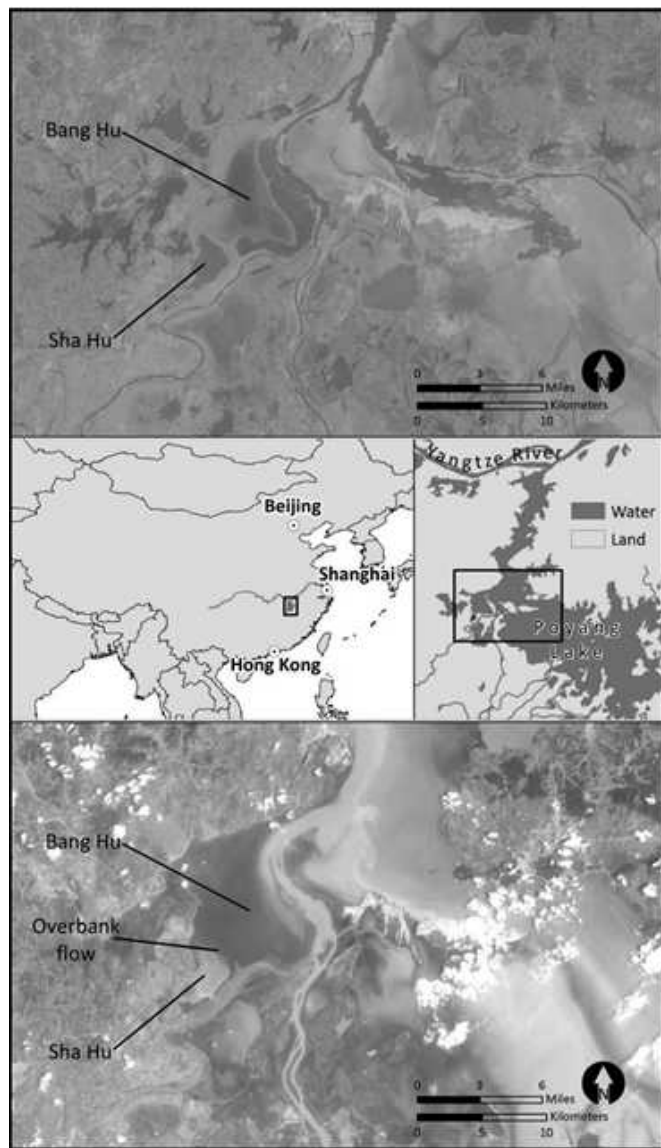


Figure 1. The location of Poyang Lake and examples of water level variation in the northwestern area of the lake between winter lows (top), where each sub-lake becomes separated from the greater Poyang Basin except by shallow channels, and summer highs (bottom), where many sub-lakes like Sha Hu become one connected hydrological system. All images from Landsat 8 (data available from the U.S. Geological Survey).

spoonbill observation data: 1) categorization of each year into an inundation class, 2) across-year comparisons of spoonbill abundance, 3) within-year spoonbill density comparisons by inundation class, and 4) within-year regression models of suitable foraging area and bird use days by inundation class. Both within-year analyses used moving averages.

Hydrological data and inundation classes

Based on Landsat 7 and 8 imagery from 2008-2015, we determined when Sha Hu sub-lake was connected to the main body of Poyang Lake through Bang Hu sub-lake (Figure 1). Satellite imagery on all available, cloud-free days were compared with the same day's

water level as measured at a staff gauge at Sha Hu (International Crane Foundation, unpublished data) to determine water levels during flooding. This inundation threshold was estimated as 16.5 m above sea level (Wu Song datum).

Long-term data were collected through a monitoring protocol shared by the International Crane Foundation (ICF) and Poyang Lake National Nature Reserve (PLNR). For hydrology, these data were collected by daily observations of water level at a central staff gauge in the Sha Hu sub-lake. Based on these data, we calculated the number of days when water depth in the Sha Hu basin exceeded the inundation threshold and summed these days for each year. Next, we categorized each year into one of three inundation classes based on how that year's number of flooded days compared to the 12-year average. All years with water levels greater than one standard deviation (SD) below the 12-year average were classified as below-average, all years with water levels within one SD were classified as average, and all years greater than one SD above the average were classified as above-average.

Spoonbill observation data

As with hydrological data, long-term observation data were collected by ICF and PLNR. Specifically, bird surveys across the entire sub-lake were conducted every seven or 10 days during the winter season (October to March). Protocol involved systematic scan sampling from a central observation point.

During these surveys, absences were not recorded and were populated a posteriori. Since bird arrival dates at Poyang varied by year, no absences were generated until after the season's first recorded bird presence. After all wintering periods were populated with absences, we calculated bird counts for each day using linear interpolation from observed counts and generated absences.

Across-year comparisons

We summed interpolated counts for each winter to get a cumulative number of spoonbills at Sha Hu. We plotted the cumulative number of spoonbills against year to investigate whether general trends existed across years, and ran a regression model using hydrologically connected days as the predictor variable to investigate whether summer conditions alone were correlated with bird abundance.

Within-year moving averages

To account for potential time-lags between changes in habitat quality and bird abundance, interpolated bird



count data were also used to calculate moving averages. If an area's food supply became unavailable or was exhausted, birds could delay their response to changing conditions and continue to search for food. Eventually, as foraging birds are unable to satisfy nutritional requirements, we expected them to move to a more productive site if one existed. However, the amount of time between habitat condition shift and bird response was unknown.

Sensitivity analysis suggested that a 10-day window provided the best duration for a moving average. For each day (hereafter, an anchor point), we calculated the average interpolated bird count using count data from the 10 days before and after that point.

To compare the amount of foraging habitat available in Sha Hu, we averaged winter water level for each window, using the same window sizes and anchor points. Winter water level was measured only at a central staff gauge located in Sha Hu, from which we extrapolated across a regional digital elevation model (Sullender *et al.* 2016). We then reclassified the resulting raster data and summed the number of cells with preferred foraging water depth, defined as a water level between 28.1 cm and 36.6 cm (Sullender *et al.* 2016). 10-day window averages of suitable foraging area and number of spoonbills were then aggregated by year and labeled by inundation class (below-average, average, and above-average).

Within-year density comparison

We divided the 10-day window average for bird abundance by a measure of average suitable habitat within the 10-day window to calculate the density of spoonbills (individuals/ha). We log-transformed data to satisfy assumptions of normality and ran a one-way ANOVA to investigate significance and a post-hoc Tukey's Honestly Significant Differences (Tukey's HSD) test to compare differences in inundation

classes. Because consecutive data points were not temporally independent, we split the dataset into 21 non-overlapping windows and ran the same tests.

Within-year regression models

To satisfy the normality assumption, we square-root transformed bird use days and used these data as the response variable in a series of 21 linear regression models, taking the moving average of suitable foraging habitat area as the predictor variable. We then calculated the percentage of models returning a significant correlation ($p < 0.05$) and calculated the overall values for each coefficient, each inundation class across all models and within only significant models. Program R (R Development Core Team 2015) was used for all analyses.

Results

Inundation classes

We categorized each year's data into three groups based on number of inundated days: below-average, average, and above-average years. 2 years (2006 and 2011) had greater than one SD below the mean number of connected days, 7 years were within one SD of the average, and 3 years (2010, 2012, and 2013) had greater than one SD above the mean number of connected days (Figure 2).

Across-year comparisons

The cumulative number of spoonbills ranged from 12,558 in 2013 to 216,395 in 2011, with an average of 109,481 birds per year (Figure 3). The cumulative number of spoonbills generally declined as connected days increased (Figure 4), although this relationship was not significant ($p = 0.26$).

Figure 2. Determining annual inundation class groups. Inundation class measured by the annual number of days when seasonal flooding connected the Bang Hu sub-lake with the Sha Hu sub-lake. The solid black line illustrates the 12-year mean number of connected days, the dotted line shows one SD less than mean, and the double line shows one standard deviation (SD) greater than mean. White points represent below-average years, grey points represent average years, and black points represent above-average years for connectivity.

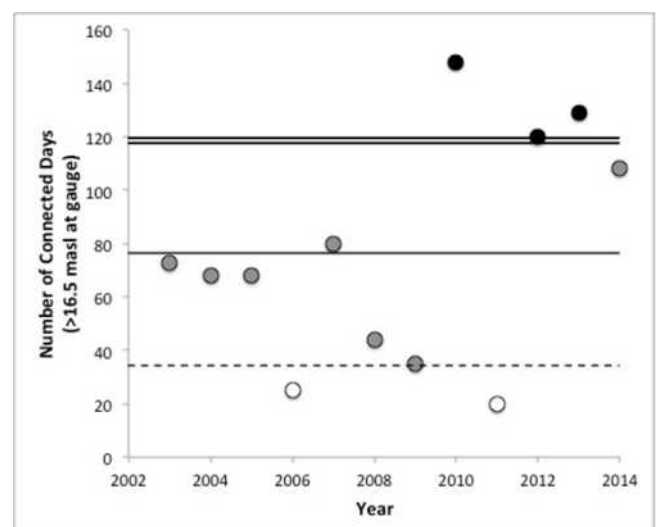
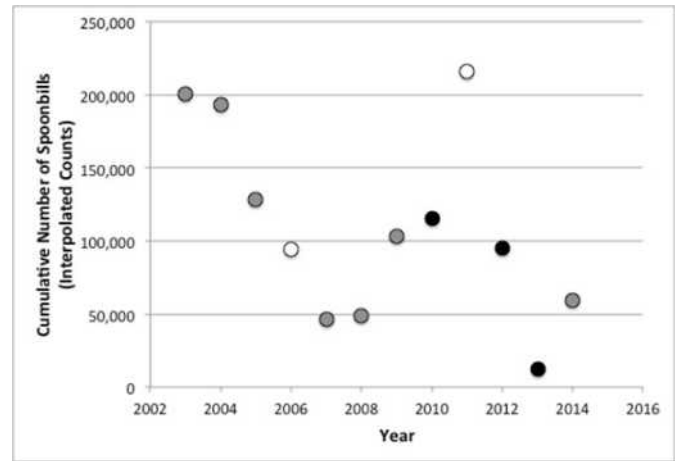


Figure 3. Cumulative number of Eurasian Spoonbills by year. Total cumulative number of Eurasian Spoonbills observed at Sha Hu sub-lake by year (2003-2014). Data points colored according to inundation class: white represents below-average inundation, gray represents average inundation, and black represents above-average inundation (see Figure 2 for inundation class definitions).



Within-year density comparisons

Although there appeared to be differences in Eurasian Spoonbill density across inundation classes (Figure 5), the use of moving windows made data non-independent. When data were aggregated into 21 separate datasets to remove overlap, no difference in spoonbill density was found among all inundation classes (minimum $p = 0.46$).

Within-year regression models

The relationship between Eurasian Spoonbill usage of Sha Hu and extent of suitable foraging area varied considerably across inundation classes (Table 1). For years with a below-average number of connected days, only two models had a significant relationship, both of which had positive slopes (Figure 6). For years with an average number of connected days, 16 of 21 models had significant positive relationships (slope > 0 ; $p < 0.05$) between suitable foraging extent and bird usage (Figure 7). In years with above-average inundation there was no relationship between spoonbill bird use days and suitable foraging extent ($p > 0.05$ for each model, $N = 21$ models, Figure 8). To remove consecutive anchor days

Figure 4. Cumulative number of Eurasian Spoonbills by duration of connectivity. Total cumulative number of Eurasian Spoonbills observed at Sha Hu sub-lake plotted against number of days when Sha Hu sub-lake was hydrologically connected with Bang Hu sub-lake (water level at Sha Hu marker > 16.5 masl). Data points colored according to inundation class: white represents below-average inundation, gray represents average inundation, and black represents above-average inundation (see Figure 2 for inundation class definitions).

from the same regression, each year's data was split into 21 sets and a linear regression model was run for each set.

Discussion

Summer conditions appear to play an important role in determining spoonbill habitat usage the following winter, and our results support most of our hypotheses. Because foraging is the most frequent behavior and comprises the highest proportion of Eurasian Spoonbill activity budget at Sha Hu (Sullender *et al.* 2016), we analyzed extent of preferred foraging habitat to test whether foraging conditions are related to summer hydrological connectivity. In years with a typical duration of flooding, spoonbills appear to be reliant on preferred foraging habitat – as more habitat is available, utilization increases. In contrast, years with below-average connectivity demonstrate a weaker but positive relationship between extent of foraging habitat and spoonbill usage. These results are consistent with our hypothesis. Contrary to our hypothesis, years with above-average connected days appear to render extent of suitable habitat an insignificant predictor of bird usage, as indicated by the discrepancy between slopes and the proportion of significant models.

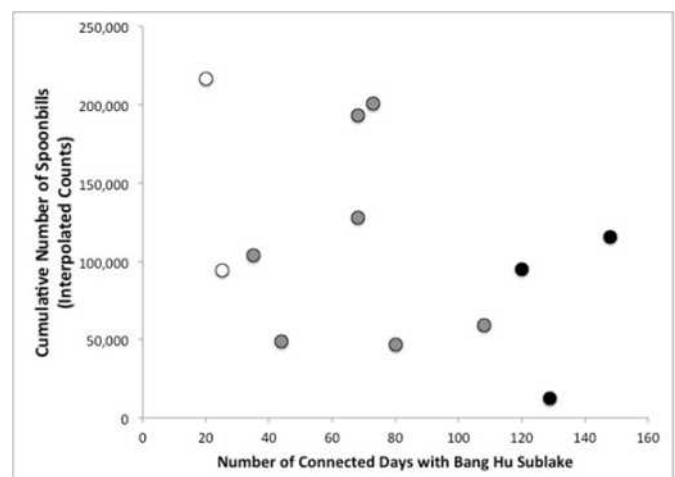
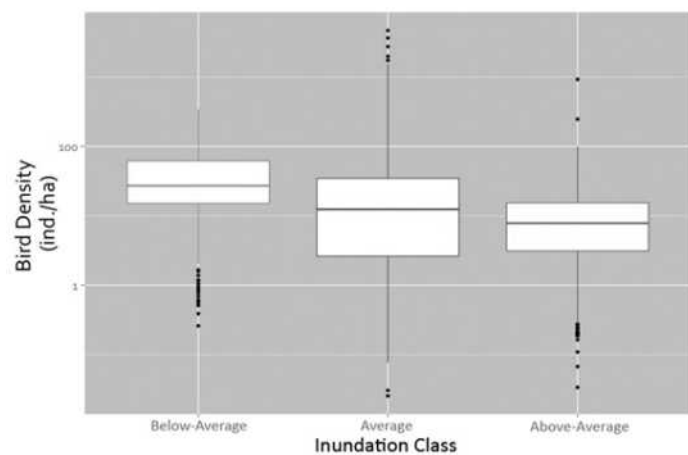


Figure 5. Boxplot of Eurasian Spoonbill density by inundation class. Each data point represents the 21-day moving average bird abundance divided by the 21-day moving average extent of suitable foraging area at Sha Hu sub-lake. Subsequent data points are non-independent and therefore, although the aggregated data as above appear to be significantly different, analysis of non-overlapping densities suggests inundation classes did not differ.



Waterbird occurrence and abundance have been widely correlated with habitat area (David 1994; Tozer *et al.* 2010; Zheng *et al.* 2015), particularly within other seasonally inundated wetland systems (e.g. Ma *et al.* 2009; Lorenz 2014) and within Poyang Lake (Sullender *et al.* 2016). In instances where bird abundance fails to reflect in-season extent of suitable habitat, myriad factors such as off-season conditions, population fluctuations, availability of alternate habitat, predation or disturbance, and changes in food resources may be altering this fundamental relationship (Tellería and Pérez-Tris 2003). Our study identifies duration of summer hydrological connectivity as a significant factor that impacts waterbird winter habitat use.

Table 1. Linear regression results of Eurasian Spoonbill use days by suitable foraging area.

Inundation class	Average intercept	Average slope	Average slope of	Number of	Percent of total
			significant regression models	significant regression models	
Below-average	18.61	0.38	0.58	2	10%
Average	9.23	0.31	0.34	16	76%
Above-average	23.42	-0.07	N/A	0	0%

Substantial evidence supports the ecological importance of seasonal flooding. Flooding both supplies the trophic system with nutrients and provides a movement vector for fish and mobile prey items (Goss *et al.* 2014). Results of seasonal flooding include higher productivity, greater fish yields, and a variety of other indicators of prey item abundance (Tockner and Stanford 2002; Ausden 2004). Conversely, disruption of normal flood dynamics – such as imposed hydrological stabilization – has been shown to negatively impact waterbird habitat use (Kingsford 2000), reduce waterbird abundance (Kingsford and Thomas 2004; Fox *et al.* 2011) and even trigger ecosystem-scale changes (Bunn and Arthington

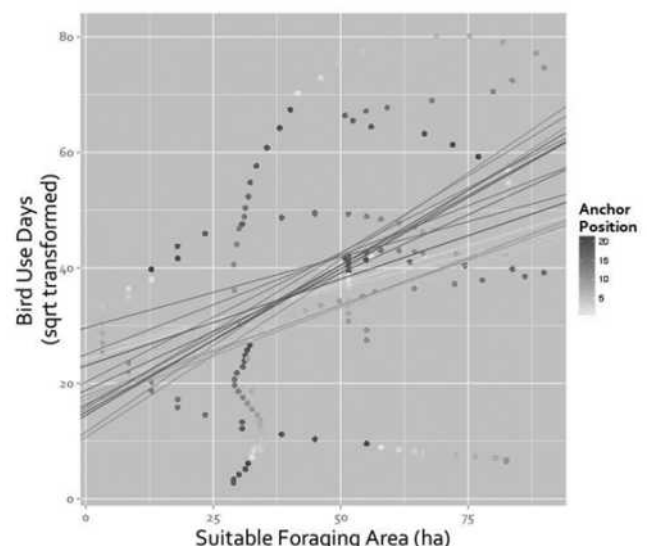
2002). Disruption of normal flood dynamics and ecological responses can also occur with extreme events such as higher than average flooding (Tryjanowski *et al.* 2009).

Our study refines the specific ecological role of flooding in the Poyang ecosystem. We used the duration of the hydrologically connected period as a proxy for the volume of nutrients, organic matter, and aquatic organisms that are transferred between the greater Yangtze River, Poyang Lake, and the Sha Hu sub-lake. With overbank flows to transport mobile prey, food items can accumulate in deeper basins such as Sha Hu. After flooding subsides, the drawdown period concentrates food items so that when wintering migrant birds arrive, there will typically be high densities of food distributed across suitable foraging habitat (Burnham *et al.* 2017). In years with average summer connectivity, spoonbill abundance was positively correlated with suitable foraging extent. Years with less than average connectivity exhibited similar but weaker relationships, and years with greater than average connectivity decoupled this relationship entirely.

There are a number of other factors that characterize flood pulse systems, such as the magnitude of flooding. During the summer of 2010, for example, Poyang Lake was exposed to such severe flooding that submerged aquatic vegetation grew poorly, if at all (Burnham *et al.* 2017), due to high water levels preventing photosynthetically active radiation from reaching lakebeds (Wu *et al.* 2009). Birds that fed on these plants were displaced and forced to adopt novel foraging strategies because typical habitats were rendered unusable (Burnham *et al.* 2017). Although Eurasian Spoonbills do not directly eat vegetation (Aguilera *et al.* 1996; Sullender *et al.* 2016), preferred prey items may depend upon plants. Since abnormally high flood waters in the Poyang ecosystem may disrupt the vegetation



Figure 6. Relationship between suitable foraging area and Eurasian Spoonbill habitat usage in years with below-average summer hydrological connectivity (2006, 2008, and 2011). Only two of the 21 models showed significant relationships. Data were partitioned into 21 non-overlapping groups and a linear regression model was constructed for each group. Groups of data are indicated by the hue of the points and corresponding regression lines.



community and decrease primary productivity (Wu *et al.* 2009), we suggest that spoonbill prey items may exhibit declines corresponding to declines in vegetative food sources under extreme flooding. However, because our study shows that absolute abundance and densities of spoonbills are not related to duration of connectivity, these declines are likely manifested in altered foraging behaviors, rather than altered habitat use and spoonbill distribution.

Additional data would allow these hypotheses to be directly tested. Future studies incorporating measurements of in-system productivity such as repeated surveys of fish biomass at a fine-scale temporal resolution would allow researchers to identify the specific relationships between flooding and food abundance within Poyang Lake. When coupled with our results, emerging statistical methods such as multivariate autoregressive models (Ives *et al.* 2003; Batt *et al.* 2017) may better identify temporally offset phenomena as sufficient long-term datasets

become available. Additionally, aside from magnitude and duration, other flood-related variables that drive ecological processes in flood pulse systems include frequency, timing, and rate of change (Poff *et al.* 1997). Although our study did not examine aspects of flooding besides duration, other factors such as magnitude have clearly identified impacts and should be assessed in combination with our findings regarding duration of flood.

Within Poyang Lake, seasonal inundation connects sub-lakes and rivers and, through physical exchanges at multiple trophic levels, creates highly productive patches. Our study indicates that the duration of summer flooding – hydrological connectivity – alters winter foraging conditions of the Eurasian Spoonbill. In particular, Eurasian Spoonbills rely on preferred habitat patches after years with below-average or average connectivity. In years with above-average connectivity, however, this relationship destabilizes, suggesting that the system's productivity and food abundance are affected by the duration of flooding.

Figure 7. Relationship between suitable foraging area and Eurasian Spoonbill habitat usage in years with average summer hydrological connectivity (2003, 2004, 2005, 2007, 2009, and 2014). Sixteen of the 21 models had significant relationships. Methods and data are as indicated in Figure 6. Groups of data are indicated by the hue of the points and corresponding regression lines.

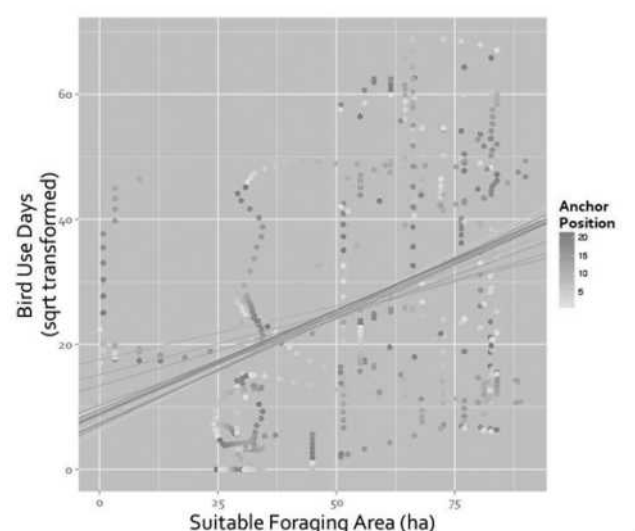
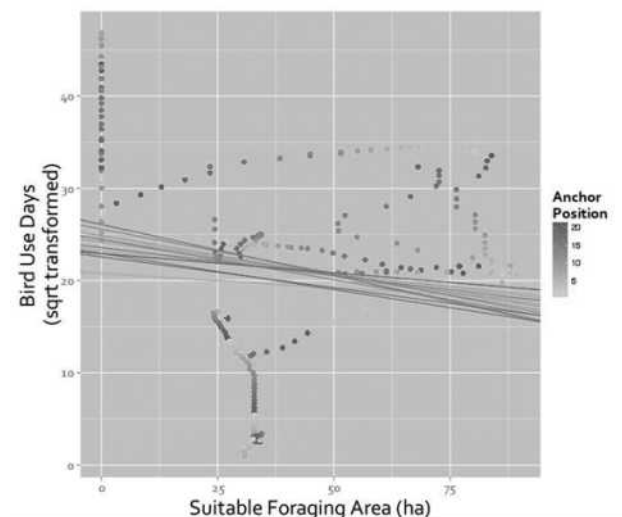


Figure 8. Relationship between suitable foraging area and Eurasian Spoonbill habitat usage in years with above-average summer hydrological connectivity (2010, 2012, and 2013). No models showed significant relationships. Methods and data are as indicated in Figure 6. Groups of data are indicated by the hue of the points and corresponding regression lines.



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