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Author(s): Benjamin Knight Sullender, Jeb Barzen and Janet Silbernagel
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Foraging Success and Habitat Selection of the Eurasian Spoonbill (*Platalea leucorodia*) at Poyang Lake, China

Benjamin Knight Sullender[1,2,*], Jeb Barzen[3] and Janet Silbernagel[1]

[1]Nelson Institute for Environmental Studies, University of Wisconsin-Madison, 550 North Park Street, Madison, Wisconsin, 53706, USA

[2]Audubon Alaska, 431 West 7th Avenue, Suite 101, Anchorage, Alaska, 99501, USA

[3]International Crane Foundation, E-11376 Shady Lane Road, P.O. Box 447, Baraboo, Wisconsin, 53913, USA

[*]Corresponding author; E-mail: bsullender@audubon.org

Abstract.—Poyang Lake is China's largest freshwater lake in summer and provides important habitat for an internationally significant assemblage of waterbirds in winter. Human-caused alterations to this system threaten to compromise the long-term viability of these bird populations due to the role of water in driving habitat suitability. Little is known, however, about the patch-scale habitat selection strategies of waterbirds within Poyang. Consequently, there is potential for spatial incongruence between protected area boundaries and key habitats given the system's high variability. This study used scan and focal sampling techniques to investigate patch selection by a wintering population of the Eurasian Spoonbill (*Platalea leucorodia*) within the Sha Hu sub-lake basin of Poyang Lake. Eurasian Spoonbills averaged higher foraging success rates in areas with water depth of 28.1-36.6 cm compared to other areas and preferred to forage in this depth class, as indicated by usage disproportionate to availability (Manly's standardized selection index = 0.817). Defining the patch-scale habitat selection of this indicator species both quantifies the impact of hydrological changes on resource availability and spatially predicts suitable areas for wintering birdlife within a dynamic environment. *Received 9 December 2015, accepted 9 May 2016.*

Key words.—Eurasian Spoonbill, foraging habitat, foraging success, habitat selection, *Platalea leucorodia*, Poyang Lake, resource availability.

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Poyang Lake, in the Jiangxi Province of eastern China, supports an internationally significant community of waterbirds, including the endangered Oriental Stork (*Ciconia boyciana*), the critically endangered Siberian Crane (*Leucogeranus leucogeranus*), and more than 300 other bird species (Kanai *et al.* 2002; Higuchi *et al.* 2004; Fang *et al.* 2006; Li *et al.* 2012). The expansive, highly variable wetland ecosystem at Poyang is sensitive to human-caused alterations such as dam construction that would potentially compromise wintering habitat for waterbirds (Wu *et al.* 2009; Wang *et al.* 2013, *in press;* Lai *et al.* 2014b).

During winter, food limitation and competition are primary structuring influences on avian populations (Martin 1987), and consequently birds allocate more time to patches that allow optimal foraging (Pyke *et al.* 1977). Pelecaniformes, including the Eurasian Spoonbill (*Platalea leucorodia*), rely on patches of suitable foraging habitat that provide abundant and accessible food items (Ntiamoa-Baidu *et al.* 1998; Herring *et al.* 2010), factors that are driven, in turn, by hydrological variation and microtopography (Gawlik 2002; Frederick *et al.* 2009). Within wetlands subject to periodic hydrological pulses, prey items are widely dispersed during seasonal inundation and concentrated during subsequent drawdown stages (Beerens *et al.* 2011; Herring and Gawlik 2011; Lorenz 2014). Waterbird communities, and wading birds in particular, may rely on this seasonal dynamic to satisfy bioenergetic requirements and maintain breeding success (Kahl 1964; Kingsford *et al.* 2004; Bino *et al.* 2015).

In Poyang Lake and other wetland ecosystems, water levels have been linked to species richness (Paillisson *et al.* 2002; Taft *et al.* 2002; Wang *et al.* 2007; Ma *et al.* 2010) and identified as a key determinant of habitat suitability for Eurasian Spoonbills (Wang *et al.* 2013) and guilds of other wading waterbirds (Ntiamoa-Baidu *et al.* 1998; Ma *et al.* 2010). These studies used a spatial scale that is suitable for basin-scale management but that is too broad to effectively determine patch-scale preferences or incorporate primary behavioral evidence (Wiens 1989; Orians and Wittenberger 1991). For example, Wang *et al.* (2013) use a single water depth measurement to approximate water levels across Poyang Lake's 3,000 km^2 extent (Feng *et al.* 2013). However, since sub-lakes and channels are managed independently by fishermen and farmers (Wang *et al. in press*), linking a central water level to overall bird abundance does not answer how water depth relates to habitat suitability at these sites.

Modeling habitat suitability of an indicator species may combine the best of both basin-wide and sub-lake scales: maintaining sensitivity to an observation-based, mechanistic understanding while also remaining relevant to the broader ecosystem. Other species of spoonbill have been used as indicators for general wetland health (Lorenz *et al.* 2009; Navedo and Garaita 2012; Ogden *et al.* 2014), and the Eurasian Spoonbill (hereafter, spoonbill) has been used as an indicator for how bird abundance is affected by wetland drainage and other land use change (Samraoui *et al.* 2011).

In this study, we examined foraging behavior of Eurasian Spoonbills in relation to water depth within the Sha Hu sub-basin of Poyang Lake. Our objectives were to investigate whether: 1) Eurasian Spoonbill foraging success changes based on water depth; and 2) Eurasian Spoonbills prefer to forage in particular water depths.

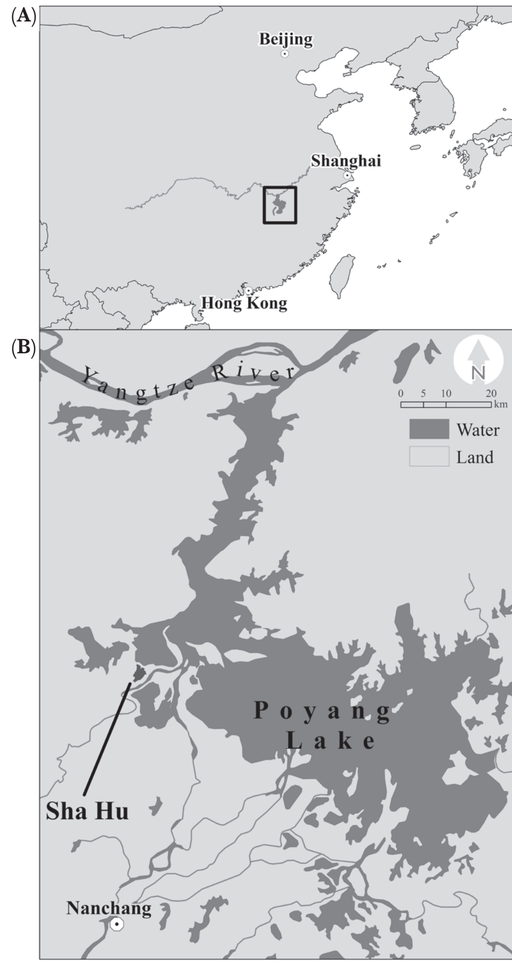

Figure 1. Study area. (A) Location of Poyang within East Asia; (B) Greater Poyang Lake and connection with Yangtze River. Sha Hu sub-lake is shown.

METHODS

Study Area

This study was conducted at Sha Hu sub-lake (29° 10′ 44″ N, 115° 56′ 1″ E), within Poyang Lake National Nature Reserve (Fig. 1). Poyang Lake is characterized by large seasonal fluctuations in water levels (Chen *et al.* 2001; Nakayama and Watanabe 2008). During the summer rainy season, the lake surface area can expand to 3,000 km^2 (Feng *et al.* 2013) from a winter dry season area as small as 700 km^2 (Zhang *et al.* 2014). Southern areas of Sha Hu are characterized by shallow, turbid water and waterlogged mudflats, while the northern sections are drier and inhabited by various species of forbs and sedges, predominantly *Carex* spp. (Zhang *et al.* 2012). Based on perennial abundance, the most likely candidate prey taxa within Sha Hu are the prawn *Macrobrachium nipponese* (Ueng *et al.* 2007) and two fish species, *Pelteobagrus fulvidraco* and *Hyporhamphus intermedius* (B. Jin, pers. commun.).

Field Observations

Field observations were conducted between 30 December 2014 and 13 January 2015. From approximately 07:00 hr until 17:30 hr, we determined Eurasian Spoonbill flock size, recorded individual behavior, and evaluated the effect of water depth on bird behavior or foraging success. We conducted observations from three primary locations distributed around the perimeter of the sub-lake. One observer conducted all surveys to reduce inter-observer bias.

Focal Sampling

We used focal sampling (Altmann 1974; Martin and Bateson 1993) to determine foraging success rates of Eurasian Spoonbills. We randomly selected a foraging bird and recorded cumulative foraging time in seconds and number of swallows for 5-min bouts. We also noted other foraging behaviors as they occurred. We chose a 5-min bout duration based on optimal sampling techniques for Black-faced Spoonbills (Choi *et al.* 2007).

Cumulative foraging time was defined as the length of time a focal bird had its mandibles in the water and demonstrated active searching behavior. We defined a swallow as the study bird raising its mandibles above the water's surface and snapping its head toward its back. We assumed this motion represented the bird moving food items from its mandibles into its oral cavity (Kemper 1995; Takano *et al.* 2014).

Scan Sampling

We used scan sampling to determine activity budgets (Martin and Bateson 1993), recording behavior at the moment of sighting for all birds in the flock that were in view. We scanned across the lake using a 10-60x magnification telescope and recorded each individual's behavior using categories of foraging, locomotion, comfort, social activity, loafing, or sleeping (Choi *et al.* 2007). We distinguished sleeping from loafing based on bill location: sleeping was recorded only when a bird's bill was stationary and located beneath a folded wing. Although display sleeping, as described in Kahl (1983), can be considered a social behavior, we classified all potential cases of display sleeping as true sleeping in this study due to the instantaneous duration of the observations.

We defined foraging as activity with the bill partially or fully submerged while attempting to locate prey, acquiring prey, or handling prey (Kemper 1995; Swennen and Yu 2005). Locomotion was divided into two secondary behaviors: flying and walking. Comfort behaviors included bathing, body shaking, preening, scratching, stretching, wing flaps, and yawning (Kahl 1983; Choi *et al.* 2007). Social activity primarily involved allopreening, but occasional occurrences of greeting and sparring were noted. Loafing was defined as the study bird remaining awake but without other activity and without its bill tucked under a wing or inserted in the water column. Pauses between discrete foraging, preening, or sleeping bouts were defined as loafing.

Water Depth and Hydrological Modeling

We recorded water depth for each individual during focal and scan sampling as one of three water depth classes defined by anatomical measurements. The hock (tibio-tarsal joint) and crural feathers were used to delineate depth classes (Yu and Swennen 2004). When an individual moved between water depths over the course of a focal sampling bout, we used the average water level over the duration of the bout.

We estimated the total area of each water depth class in Sha Hu by interpolating water depth measurements across a digital elevation model of the basin. To generate the digital elevation model, we used baseline water depth measurements (International Crane Foundation, unpubl. data) as input for kriging (using a 12-point radius and a spherical semivariogram model; Maynou *et al.* 1996). We then calculated the average water depth in cm for the study period and used this to reclassify each 11.6-m x 11.6-m cell into one of the three depth classes. Finally, we aggregated cells within the same depth class and converted each class' total area into ha. We performed all spatial analysis in ArcGIS (Environmental Systems Research Institute 2011).

Data Transformation and Analysis

For each scan sampling bout, we calculated the percentage of the total flock engaging in each behavior. We further partitioned these percentages by depth class. For focal sampling data, we omitted all foraging bouts with less than 3 min of cumulative foraging behavior and calculated the number of swallows per min of foraging.

For both scan and focal observations, we checked for temporal autocorrelation by using semivariograms, substituting time distance between observations for the usual spatial distance (Jauhiainen and Korhonen 2005). We compared our observed variograms to thresholds computed from randomly generated variograms to determine whether temporal autocorrelation existed. Additionally, we checked for normality using quantile-quantile plots. When necessary, we transformed data sets that violated the normality assumption.

We used an analysis of variance (ANOVA) and Tukey's Honest Significant Differences (HSD) test to compare foraging success rates between water depths. To determine foraging habitat preference, we first used a chi-square goodness-of-fit test to examine differences between availability and usage (Byers *et al.* 1984). We then calculated Manly's standardized selection index for each depth class (Manly *et al.* 2002). Manly's index estimates the probability that a given depth class will be selected if all classes are equally available (Manly *et al.* 2002; Lantz *et al.* 2011). We then constructed simultaneous confidence intervals that were adjusted for the number of depth classes (Byers *et al.* 1984) and compared these intervals to observed habitat usage to determine whether the null hypothesis of proportional usage was accepted or rejected (Neu *et al.* 1974; Garshelis 2000). We used the statistical program R (R Development Core Team 2013) for analyses.

RESULTS

Classification of Water Depth

We grouped observed water depths into three classes: shallow, intermediate, and deep. Shallow water was defined as water levels ranging from the toes to the hock, intermediate depth water was defined as above the hock to the crural feathers, and deep water was defined as above the crural feathers to the deepest observed water, halfway up the abdomen. Based on Eurasian Spoonbill specimen measurements (n = 5) and methods described in Sullender (2015), the shallow depth class ranged from 0.5 cm to 16.7 cm, the intermediate depth class ranged from 16.8 to 28.0 cm, and the deep depth class ranged from 28.1 to 36.6 cm.

Hydrological Conditions and Extent of Water Depth Classes

Given extensive inter-annual variation in the seasonal water levels of Poyang Lake (Wu *et al.* 2009), we assessed whether conditions during the observation period were consistent with those typically observed at Sha Hu in January. Water depth, as measured at a central stationary marker, was 49.3 cm, compared with a 15-year average of 52.3 cm (SD = 26) for the same December-January time period. In 2014, the maximum summer water depth was 364.3 cm, similar to the 15-year average maximum of 366.3 cm (SD = 85; Jin *et al.* 2012).

Within the basin of Sha Hu, a total of 330.6 ha were inundated during the study period. Of these, 66.1 ha (20.0%) were classified as the deepest water depth class, 100.6 ha (30.4%) were classified as intermediate depth, and 137.7 ha (41.7%) were classified as shallow. The remaining 26.1 ha (7.9%) exceeded the maximum observed foraging depth of Eurasian Spoonbills.

General Behaviors and Activity Budget

We recorded 197 focal samples and 137 scan samples of Eurasian Spoonbills, stratified across all daylight hours, with the earliest scan sample starting at 07:03 hr and the latest starting at 17:19 hr (Fig. 2). We recorded water depth and behavior for each individual during 61 of the 137 scan samples and recorded only behavior during the other scan samples. Across all scan samples, observed flock size ranged from nine to 2,548 individuals with a mean of 813 individuals. Of the 111,447 scan samples of Eurasian Spoonbills sampled at Sha Hu, most individuals were recorded as foraging, sleeping, or loafing (Table 1). Foraging behavior varied by time of day but not in a consistent pattern (Fig. 2). In the morning, 55.6% of observed birds were sleeping between 07:00 and 08:00 hr. In the evening (between 16:00 and 17:30 hr), more than 58.7% of observed birds were foraging.

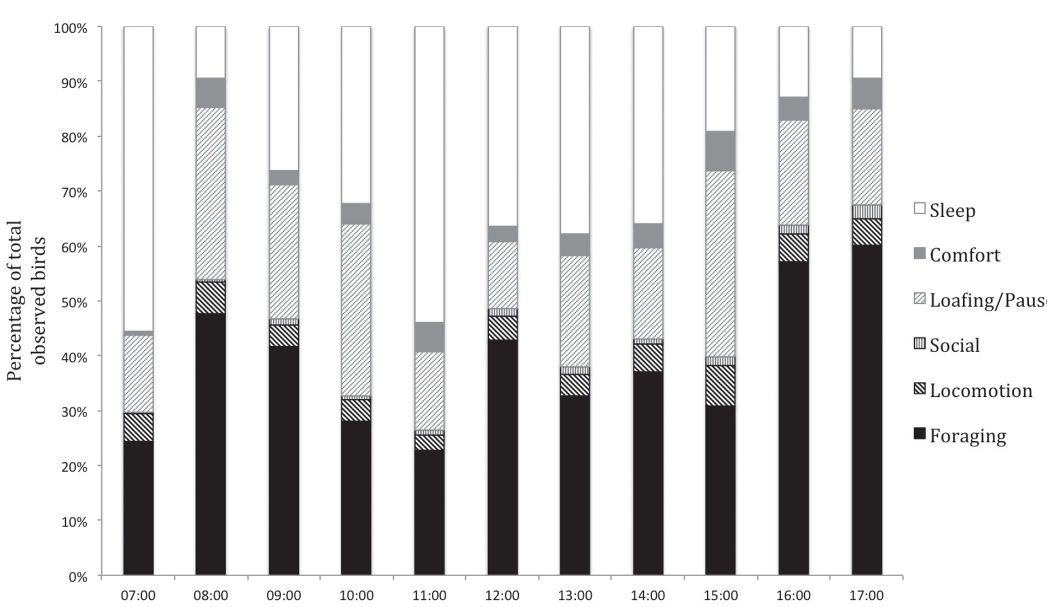

Figure 2. Activity budget of Eurasian Spoonbills at Sha Hu sub-lake in Poyang Lake, China. All observations were aggregated by hour across all observation days (30 December 2014-13 January 2015). Total number of samples per hour are shown above chart.

Table 1. Frequency of observed behaviors of Eurasian Spoonbills. Scan sample data was pooled across all observations for the entire study period (*n* = 137; December 2014-January 2015).

Frequency	Foraging	Flying	Walking	Social	Loafing	Comfort	Sleeping	Total
Number of Birds	40,558	4,037	915	1,271	24,214	3,978	36,474	111,447
Percentage of Total	36.4%	3.6%	0.8%	1.1%	21.7%	3.6%	32.7%	100%

Foraging Success Rates in Relation to Water Depth

Eurasian Spoonbill foraging success rates differed significantly across water depth classes (data square-root transformed; ANOVA, $F_{2,129}$ = 14.45, P < 0.001). Spoonbills had greater average foraging success in deeper water (0.70 swallows per min, n = 81) than in either shallow water depths (0.41 swallows per min, P < 0.05, n = 19) or intermediate water depths (0.24 swallows per min, P < 0.001, n = 32; Fig. 3). Foraging success rates at intermediate and shallow water depths did not differ (P = 0.274).

Water Depths Preferred for Foraging

We observed more Eurasian Spoonbills foraging in deeper water areas of Sha Hu and fewer foraging in the shallowest areas. From the 61 scan samples including water depth, 853 spoonbills foraged in shallow water, as compared to 6,014 foraging in intermediate depths and 19,487 foraging in deep water. No spoonbills were observed in water deeper than 36.6 cm.

Habitat use differed from availability (surface area of depth class; P < 0.001, χ^2_3 = 190.3). The 95% confidence intervals for Manly's standardized selection index at each depth class did not contain the availability value for the shallow, intermediate, or deep depth classes (Table 2), and therefore we rejected the null hypothesis of proportionate foraging (Manly *et al.* 2002). Eurasian Spoonbills preferred foraging within the deep depth classes and avoided foraging in the shallow and intermediate depth classes (Manly's selection index for deep = 0.817, intermediate = 0.166, and shallow = 0.017). Due to no Eurasian Spoonbill use of areas deeper than 36.6 cm, we excluded this class when generating confidence intervals (Manly *et al.* 2002).

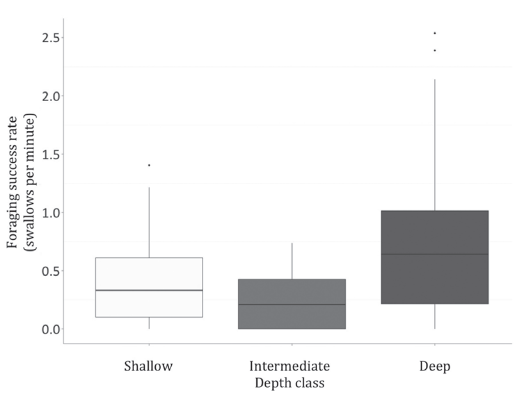

Figure 3. Box plot of foraging success rates of Eurasian Spoonbills in different water depth classes at Sha Hu sub-lake in Poyang Lake, China. The dark line represents the median, the bottom edge of the box represents the first quartile, the top edge of the box represents the third quartile, the whiskers bound 1.5 times the inter-quartile range, and points represent outliers. Shallow depth class defined as 0.5-16.7 cm of water, intermediate depth class defined as 16.8-28.0 cm of water, and deep depth class defined as 28.1-36.6 cm of water.

DISCUSSION

Deep water (28.1-36.6 cm) provided the preferred habitat for Eurasian Spoonbills and, while in deep water, foraging spoonbills were more successful. The Eurasian Spoonbill requires winter water levels that allow the bird to maintain a wading posture, freely sweep its bill through the water column, and reach to near the substrate (Weihs and Katzir 1994; Kemper 1995; Aguilera *et al.* 1996; Yu and Swennen 2004). If water levels are too high for Eurasian Spoonbills to reach close enough to the lakebed or are too low for spoonbill prey to persist in the winter, foraging conditions are compromised.

Wading birds such as the Eurasian Spoonbill respond to changes in environmental conditions most strongly through habitat selection (Lantz *et al.* 2011), so as hydrology

Table 2. Habitat selection by foraging Eurasian Spoonbills across water depth classes using Manly's selection index with 95% confidence intervals. Usage is the proportion of spoonbills observed in a given depth class, and availability represents the area of that depth class as a proportion of total area. Foraging preference is indicated by selection index greater than availability.

Depth Class	Depth Range (cm)	Usage	Availability	Manly's Selection Index	Confidence Intervals	
					Lower	Upper
Shallow	0.5-16.7	0.032	0.417	0.017	0.000[a]	0.053
Intermediate	16.8-28.0	0.228	0.304	0.166	0.064	0.267
Deep	28.1-36.6	0.739	0.200	0.817	0.711	0.922
Exceeds Maximum Foraging Depth	36.7-43.3	0.000	0.079	0.000	–[b]	–[b]

[a]Negative confidence intervals replaced with 0.000.

[b]Because no Eurasian Spoonbills were observed in water deeper than 36.6 cm, the selection index for this class must be regarded as indicative only and was excluded from confidence interval calculations.

shifts over the course of a season, birds will redistribute to track preferred conditions (Gawlik 2002). Changes in wintering habitat and resultant shifts in food availability and abundance impact breeding success in subsequent seasons and ultimately population demography (Drent and Daan 1980; Ma *et al.* 2009; Lorenz 2014). Effective conservation, therefore, relies on provision of these suitable foraging habitats, and by being able to identify these areas at a patch scale, protection mechanisms can be spatially targeted.

Across Poyang Lake and specifically within Sha Hu, small water control structures exist and are managed primarily by fishermen (Wang *et al. in press*). This creates the potential to manage lakes and sub-lakes at water depths deemed optimal for waterbirds, a concept that appears to be supported by studies such as ours and correlative analyses such as Wang *et al.* (2013). However, relying on manipulation of water levels to support ecological function fails to acknowledge the central role of natural hydrological variability and connectivity (Kingsford 2000). As seen in flood-pulse systems worldwide, hydrological connectivity—the summer flooding stage at Poyang Lake—gives rise to immense productivity (Jenkins and Boulton 2003; Thoms 2003). The fall drawdown period at Poyang Lake concentrates prey into smaller sub-basins such as Sha Hu in a manner similar to other wetland systems (Gawlik 2002; Wu *et al.* 2009; Beerens *et al.* 2011), and this seasonal dynamic has been linked to the integrity of waterbird communities in analogous ecosystems (Bunn and Arthington 2002; Kingsford *et al.* 2004).

This study provides insight into habitat selection and foraging ecology within a hydrologically normal year at Poyang Lake. These relationships may be altered following severe flooding or severe droughts (Barzen 2012). Such major disturbances redistribute suitable habitat (Gawlik 2002) and have been observed to shift wading bird distribution outside the boundaries of Poyang Lake's protected areas (J. Burnham, pers. commun.). Anthropogenic alterations such as sand dredging (de Leeuw *et al.* 2009) and dam construction (Lai *et al.* 2014a; Zhang *et al.* 2014) may compound the effects of Poyang Lake's natural hydrological variability and result in further spatial incongruence between protected area boundaries and suitable waterbird habitat.

To understand when and where waterbird displacement will occur, an improved understanding of habitat selection across seasons and across hydrological conditions is essential. Future study, particularly incorporating bird abundance data from other areas of Poyang Lake such as Nanjishan Nature Reserve, may reveal if the deep depth class suggested in this study is representative of the Eurasian Spoonbill's ideal foraging habitat or if the distribution of ideal habitat is driven more by seasonal variability than by winter water level. Tracking waterbird distribution in response to hydrological variability would extend the suitability models presented here to a broader range of conditions and allow protected area managers to identify key foraging areas across the Poyang Lake basin in concert with this system's natural dynamics.

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