



# The Spatial-Temporal Dynamics and Niche Separation of Overwintering Shorebirds in Nanji Wetland National Nature Reserve of Poyang Lake, China

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## ABSTRACT

In January of each year from 2015 to 2020, a survey of shorebirds in 13 sampled areas of Nanji Wetland National Nature Reserve of Poyang Lake was conducted to study the spatial-temporal distribution and niche separation of shorebirds over 6 years. Three families and 11 species were recorded. Scolopacidae had the highest number of species (7), which accounted for 63.64% of all species of shorebirds surveyed. From 2015 to 2020, the number of species (5–7) showed little variation, indicating that the reserve could provide a stable wintering environment for a variety of shorebirds. The number of dominant shorebird species showed large variation over spatial and temporal scales, indicating that the birds would change their spatial distribution according to changes in micro-habitat. Spotted Redshank *Tringa erythropus* was distributed across 13 sampled areas with relatively large population sizes, and the temporal niche (0.880) and spatial niche (0.798) were wide. Northern Lapwing *Vanellus vanellus* was distributed in 12 sampled areas with small but relatively stable population sizes, and the temporal niche (0.972) and spatial niche (0.830) were the widest. The results showed that the adaptability of Northern Lapwing and Spotted Redshank in Poyang Lake was stronger and they were more widely distributed than other shorebirds. The niche overlap in spatial and temporal dimensions of these two species was the highest. They had niche separation to decrease competition and improve coexistence, mainly through differences in food composition, foraging mode, and micro-habitat. The foraging habits of Pied Avocet *Recurvirostra avosetta* are similar to those of Spotted Redshank, and the spatial and temporal niche overlap with Spotted Redshank was relatively high. These species had spatial niche separation to decrease competition and improve coexistence, mainly through differences in foraging mode and micro-habitat. The results indicate that the diversity of micro-habitat types can provide habitat for more shorebirds and decrease competition. Therefore, protection of diverse micro-habitats can maintain a high diversity of shorebirds.

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## Authors' Contribution

SMQ and ZJH designed and revised the paper. ZJH, ZYJ, YFC and SMQ collected and analyzed the data. ZJH wrote the paper.

## Key words

Poyang Lake, Nanji Wetland, Shorebirds, Niche separation

## INTRODUCTION

As an important ecosystem on Earth, wetlands provide an important habitat and food resources for shorebirds (Cui and Deng, 2007). Poyang Lake is located in the East Asian-Australasian Flyway and is the most important wintering place for migratory shorebirds in China. The Poyang Lake wetland area is large, and the wetland ecosystem is complete and continuous (Cui, 2004; Lu *et al.*, 2021).

Shorebirds are small and medium-sized wading birds with long-distance migration habits. Shorebirds include water birds such as Charadriidae, Scolopacidae, and Recurvirostridae, most of which rely on wetland networks of wintering sites, breeding sites, and migration stopover sites to complete their life cycle (Heng *et al.*, 2011; Novcic, 2016). Shorebirds are the main group of overwintering and migratory water birds in many areas; they are also an important part of wetland bird diversity and play important roles in maintaining the stability of wetland ecosystems (He *et al.*, 2019).

Shorebirds are sensitive to habitat changes. Their adaptability to changes in water level and micro-habitat is weaker than Anseriformes; therefore, they can act as important indicators for monitoring changes in wetland ecosystems (Howes and Bakewell, 1989; Zeng *et al.*, 2021). Previous studies of shorebirds evaluated habitat utilization and selection (Hou *et al.*, 2013; Monk *et al.*, 2020), foraging behavior (Feng *et al.*, 2019; Fonseca and

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Navedo, 2020), migration behavior (Hui *et al.*, 2009; Xiao *et al.*, 2021), behavioral rhythm (Shen *et al.*, 2016), and population or community characteristics (Li *et al.*, 2015; Koleek *et al.*, 2021; Warnock *et al.*, 2021). In recent years, because of the impact of human activities and invasion of alien species, the loss and degradation of the foraging habitats of shorebirds has become serious, and their survival status has been greatly affected (Heng *et al.*, 2011; Koleček *et al.*, 2021). Previous studies of shorebirds were mainly concentrated in coastal wetlands, and there has been less research on shorebirds in inland lakes (Hou *et al.*, 2013; Feng *et al.*, 2019). There has been no research on the spatial and temporal distributions of shorebirds in Poyang Lake during the overwintering period. Therefore, it is necessary to study the spatial-temporal distribution and dynamics of shorebirds in Poyang Lake.

In this study, we surveyed the overwintering shorebirds in Nanji Wetland National Nature Reserve of Poyang Lake. The objectives of our study were to: (1) preliminarily infer the species composition and spatial-temporal distribution dynamics of shorebirds in this reserve, (2) clarify the spatial-temporal niche separation of shorebirds in this reserve, and (3) provide some basic data for the effective protection of and future research on shorebirds.

## MATERIALS AND METHODS

### Study area

Poyang Lake is located in the north of Jiangxi Province. It is the largest freshwater lake in China. It is fed by Ganjiang River, Fuhe River, Xinjiang River, Raohe River and Xiuhe River and connects with the Yangtze River, forming the Poyang Lake water system. It is a typical subtropical monsoon climate (Wang *et al.*, 2020b). Nanji Wetland National Nature Reserve of Poyang Lake (28°52'21" - 29°06'46"N, 116°10'24" - 116°23'50"E) is located in Nanji Township, Xinjian County, Jiangxi Province, the south of Poyang Lake. It is located in the delta formed by the alluvial flow of the North Branch, middle branch and South Branch of Ganjiang River. It is mainly composed of islands, lakes and beaches, and the annual surface inundation time is 2-5 months (Wang *et al.*, 2020a). The complex and diverse habitats in the delta make the reserve rich in biodiversity. It is an open and complex wetland and one of the most important habitats for many overwintering water birds (Shao *et al.*, 2016). Surveys were performed in 13 sampled areas: Zhanbei Lake, Sanhu Lake, Chang Lake, Fengwei Lake, Sanniwan, Baisha Lake 2, Baisha Lake 1, Nanshen Lake, Xiabeijia, Shangbeijia, Shangbeijia 2, Shentangzi Lake and Beishen Lake.

### Data collection

In January of each year from 2015 to 2020, a survey of shorebirds in 13 sampled areas of Nanji Wetland National Nature Reserve of Poyang Lake was conducted by using the direct count method. Birds were observed using a Swarovski monocular telescope (20-60 x 80 mm) or binocular telescope (8 x 42 mm), observing and recording the species and number of shorebirds within about one km of the sampled area. We adopted the combination of accurate counting method and estimation method. The accurate counting method was adopted for the small population and the group statistics method was adopted for the large population (He *et al.*, 2019). At each observation site shorebirds were counted for 10-20 min, and the observation time of a large population was moderately prolonged. Bird classification was based on A Checklist on the Classification and Distribution of the Birds of China (3<sup>rd</sup> Edition) (Zheng, 2017). The number of sampled area referred to the number of sample areas where shorebirds were encountered during the survey period. The cumulative number of sampled area referred to the total number of sampled areas where shorebirds were encountered over 6 years.

### Data analysis

Niche breadth (Zhu *et al.*, 1998; Zhang, 2004)

$$H = -(\sum_i P_i \log_2 P_i) / H_{max}$$

H represents niche breadth;  $P_i$  represents the  $i^{th}$  resource grade account for the total resource grades.

Niche overlap (Zhu *et al.*, 1998; Zhang, 2004).

$$A_{xy}(D) = 1 - \frac{1}{2} \sum_{i=1}^n |P_{xi} - P_{yi}|$$

$P_{xi}$  and  $P_{yi}$  represent the proportion of the  $i^{th}$  resource grade for species  $x$  and  $y$  for the total resource (two dimensions: habitats and water depth), respectively.  $A_{xy}$  (overlap value) ranges from 0 (no overlap) to 1 (complete overlap).

Niche breadth and overlap were measured in spatial and temporal dimensions. Time was divided into six years: 2015, 2016, 2017, 2018, 2019, and 2020. Space was divided into 13 areas: Zhanbei Lake, Sanhu Lake, Changhu Lake, Fengwei Lake, Sanniwan, Baisha Lake 1, Baisha Lake 2, Nanshen Lake, Xiabeijia, Shangbeijia 1, Shangbeijia 2, Shentangzi Lake, and Beishen Lake. The niche overlap of five species that cumulatively represented more than 10% of the total birds observed in a single year was measured in spatial and temporal dimensions.

## RESULTS

### *Spatial-temporal distribution and niche breadth*

From 2015 to 2020, a total of 3 families and 11 shorebird species were recorded in Nanji Wetland National Nature Reserve of Poyang Lake. Scolopacidae had the highest number of species (7), accounting for 63.64% of all shorebirds surveyed (Table I). Eurasian curlew *Numenius arquata* is listed in the second category of China's nationally protected bird species. The black-tailed godwit *Limosa limosa* and Eurasian curlew are rated as near-threatened species in the IUCN red list (Table I).

Five to seven species of shorebirds were recorded annually from 2015–2020. The greatest number of species (7) was recorded in 2016 and the fewest (5) in 2019 and 2020 (Table I). The pied avocet, northern lapwing, and spotted redshank were recorded every year. Little ringed plover *Charadrius dubius*, Kentish plover *Charadrius alexandrinus*, common snipe *Gallinago gallinago*, and Eurasian curlew were each recorded in one year only. The species of shorebirds that cumulatively accounted for more than 10% of all birds observed in a single year were pied avocet, northern lapwing, black-tailed godwit, spotted redshank, and dunlin *Calidris alpina*. The spotted redshank had the greatest abundance in 2015 (85.38%). Among three species whose cumulative number of sampled areas was more than 15, among which spotted redshank occurred in 43 sampled area-times, followed by northern

lapwing (32 sampled area-times) (Table I). Three species were found in more than 5 sampled areas of these, spotted redshank occurred in all 13 sampled areas, followed by northern lapwing, which occurred in 12 sampled areas (Table I).

Spotted redshank was distributed in 13 sampled areas, but the population size in each sampled area was quite different. Northern lapwing was detected in 12 sampled areas, and the population size in various sampled areas was small. The pied avocet was distributed in 11 sampled areas with large population size. Little ringed plover, Kentish plover, common snipe, Eurasian curlew, and dunlin were all distributed in only one sampled area each; dunlin had a large population size and the other four species had a small population size (Table II).

Northern lapwing (0.972), spotted redshank (0.880), green sandpiper *Tringa ochropus* (0.869), and pied avocet (0.671) had high temporal niche breadth (more than 0.600) in different years in Nanji Wetland National Nature Reserve of Poyang Lake. The temporal niche breadth of other species was narrow; the niche breadths of little ringed plover, Kentish plover, common snipe, and Eurasian curlew were 0 (Table I). Northern lapwing (0.830) and spotted redshank (0.798) had high spatial niche breadth (more than 0.600) in different sampled areas. The spatial niche breadth of other species was narrow; the niche breadth of little ringed plover, Kentish plover, common snipe, Eurasian curlew, and dunlin was 0 (Table II).

**Table I. Abundance and niche breadth of shorebirds overwintering in Nanji Wetland National Nature Reserve of Poyang Lake from every January from 2015- 2020.**

| Species                        | Year             |                  |                  |                  |                  |                  | Cumulative<br>number of<br>sampled areas | Number of Niche<br>sampled<br>areas | breadth |
|--------------------------------|------------------|------------------|------------------|------------------|------------------|------------------|------------------------------------------|-------------------------------------|---------|
|                                | 2015<br>(n=3452) | 2016<br>(n=3048) | 2017<br>(n=6271) | 2018<br>(n=7872) | 2019<br>(n=8071) | 2020<br>(n=4782) |                                          |                                     |         |
| Recurvirostridae               |                  |                  |                  |                  |                  |                  |                                          |                                     |         |
| <i>Recurvirostra avosetta</i>  | 4.82% /1*        | 8.82% /2         | 73.06% /2        | 75.33% /4        | 34.28% /8        | 2.07% /2         | 19                                       | 11                                  | 0.671   |
| Charadriidae                   |                  |                  |                  |                  |                  |                  |                                          |                                     |         |
| <i>Vanellus vanellus</i>       | 8.88% /9         | 4.34% /4         | 3.14% /5         | 3.25% /6         | 4.75% /5         | 12.38% /3        | 32                                       | 13                                  | 0.972   |
| <i>Charadrius dubius</i>       |                  | 0.04% /1         |                  |                  |                  |                  |                                          | 1                                   | 0.000   |
| <i>Charadrius alexandrinus</i> |                  |                  |                  | 0.04% /1         |                  |                  | 1                                        | 1                                   | 0.000   |
| Scolopacidae                   |                  |                  |                  |                  |                  |                  |                                          |                                     |         |
| <i>Gallinago gallinago</i>     |                  | 0.18% /1         |                  |                  |                  |                  | 1                                        | 1                                   | 0.000   |
| <i>Limosa limosa</i>           | 0.46% /1         | 77.70% /2        |                  |                  | 10.18% /1        |                  | 4                                        | 4                                   | 0.324   |
| <i>Numenius arquata</i>        |                  |                  |                  |                  |                  | 0.29% /1         | 1                                        | 1                                   | 0.000   |
| <i>Tringa erythropus</i>       | 85.38% /8        | 8.82% /6         | 22.92% /8        | 22.92% /9        | 50.76% /9*       | 30.71% /3        | 43                                       | 13                                  | 0.880   |
| <i>Tringa nebularia</i>        | 0.40% /3         |                  | 0.06% /2         | 0.11% /2         |                  |                  | 7                                        | 5                                   | 0.557   |
| <i>Tringa ochropus</i>         | 0.06% /1         | 0.11% /2         | 0.02% /1         | 0.03% /1         | 0.03% /1         |                  | 6                                        | 5                                   | 0.869   |
| <i>Calidris alpina</i>         |                  |                  | 0.80% /1         |                  |                  | 54.56% /1        | 2                                        | 1                                   | 0.078   |

\*cumulative number proportion at a single year/ number of sampled areas.

**Table II. Spatial distribution and niche breadth of shorebirds overwintering in Nanji Wetland National Nature Reserve of Poyang Lake.**

| Species                        | Zhanbei Lake | Sanhu Lake | Chang-hu Lake | Feng-wei Lake | Sanni-wan | Baisha Lake 2 | Baisha Lake 1 | Nan-shen Lake | Xia-beijia | Shang-beijia | Shang-beijia 2 | Shen-tangzi Lake | Beishen Lake | Niche breadth |
|--------------------------------|--------------|------------|---------------|---------------|-----------|---------------|---------------|---------------|------------|--------------|----------------|------------------|--------------|---------------|
| <b>Recurvirostridae</b>        |              |            |               |               |           |               |               |               |            |              |                |                  |              |               |
| <i>Recurvirostra avosetta</i>  | 4*           | 1700       | 100           | 18            | 7910      | 150           | 500           | 2             |            | 54           |                | 170              | 2007         | 0.467         |
| <b>Charadriidae</b>            |              |            |               |               |           |               |               |               |            |              |                |                  |              |               |
| <i>Vanellus vanellus</i>       | 8            | 10         | 105           | 30            | 264       | 74            | 140           | 288           | 275        | 222          |                | 57               | 45           | 0.830         |
| <i>Charadrius dubius</i>       |              |            | 1             |               |           |               |               |               |            |              |                |                  |              | 0.000         |
| <i>Charadrius alexandrinus</i> |              |            |               |               |           |               |               |               |            |              |                |                  | 3            | 0.000         |
| <b>Scolopacidae</b>            |              |            |               |               |           |               |               |               |            |              |                |                  |              |               |
| <i>Gallinago gallinago</i>     | 5            |            |               |               |           |               |               |               |            |              |                |                  |              | 0.000         |
| <i>Limosa limosa</i>           |              | 1420       | 15            |               | 700       | 800           |               |               |            |              |                |                  |              | 0.419         |
| <i>Numenius arquata</i>        |              |            |               | 8             |           |               |               |               |            |              |                |                  |              | 0.000         |
| <i>Tringa erythropus</i>       | 94           | 2407       | 2298          | 664           | 447       | 292           | 852           | 1423          | 23         | 139          | 4              | 252              | 1579         | 0.798         |
| <i>Tringa nebularia</i>        |              | 1          |               | 1             | 13        |               |               |               | 3          |              |                |                  | 7            | 0.471         |
| <i>Tringa ochropus</i>         | 3            | 2          |               |               |           |               | 1             |               |            |              |                | 4                |              | 0.499         |
| <i>Calidris alpina</i>         |              |            | 1580          |               |           |               |               |               |            |              |                |                  |              | 0.000         |

\*refers to the cumulative number of species within 6 years in various sampled areas.

#### *Spatial-temporal distribution dynamics and niche overlap of dominant species*

In this study, the spatial-temporal distribution of five species that cumulatively represented more than 10% of observed birds in a single year was analyzed. The number of dominant species tended to increase with time. The greatest number of species occurred in 2019 and 2020, with 3 dominant species, and the fewest occurred in 2015 and 2016, with only 1 dominant species (Table I).

The population size of pied avocet and spotted redshank and number of sampled areas in which they were found were relatively large; therefore, they were considered relatively stable dominant species. The annual population size of pied avocet (58–5286) and spotted redshank (252–3492) showed drastic fluctuations (Table III). The distribution of pied avocet in Sanniwan was relatively stable, and the encounter rate in other sampled areas was very unstable (Table III). The spotted redshank was consistently distributed in some sampled areas every year. Northern lapwing showed little variation in annual population size (124–347) among the dominant species, and was consistently distributed in some sampled areas every year. The population size and distribution in sampled areas of black-tailed godwit and dunlin was extremely unstable, with strong randomness (Table III).

Of the 10 species pairs with spatial niche overlap in different lakes in the Nanji Wetland National Nature

Reserve of Poyang Lake, the following had niche overlap values of more than 0.400: Northern lapwing and spotted redshank (0.458), and pied avocet and spotted redshank (0.412) (Table IV).

## DISCUSSION

#### *Species composition*

A total of 3 families and 11 species were recorded in Nanji Wetland National Nature Reserve of Poyang Lake, which was higher than the previous records of 8 species at Poyang Lake National Nature Reserve and 6 species at Kangshan Migratory Bird Nature Reserve (Zhu *et al.*, 2012; Zhi *et al.*, 2020), and similar to the previous records of 12 species in Duchang Migratory Bird Nature Reserve (Zhi *et al.*, 2020). As this survey lasted for a long time, the number of species recorded was more complete. Compared with coastal wetlands, the number of species in this study was lower than the previous records of 22 species in Yancheng Nature Reserve (Hou *et al.*, 2013) and 32 species in mangrove wetlands in Leizhou Peninsula (Liu *et al.*, 2015). This is because shorebirds mainly forage for the benthic biota in wetlands; coastal wetlands have a wide vision, large area, and food resources that are richer and easier to obtain than in inland lakes (Chen *et al.*, 2015).

**Table III. The temporal and spatial distribution dynamics of 5 dominant shorebirds in Nanji Wetland National Nature Reserve of Poyang Lake.**

| Year | Sample area     | Species                        |                          |                       |                          |                         |
|------|-----------------|--------------------------------|--------------------------|-----------------------|--------------------------|-------------------------|
|      |                 | <i>Recur-virostra avosetta</i> | <i>Vanellus vanellus</i> | <i>Limo-sa limosa</i> | <i>Tringa erythropus</i> | <i>Cal-idris alpina</i> |
| 2015 | Zhanbei Lake    | 0                              | 3                        | 0                     | 40                       | 0                       |
|      | Sanhu Lake      | 0                              | 8                        | 0                     | 1300                     | 0                       |
|      | Changhu Lake    | 0                              | 16                       | 15                    | 1000                     | 0                       |
|      | Fengwei Lake    | 0                              | 0                        | 0                     | 90                       | 0                       |
|      | Sanniwan        | 157                            | 24                       | 0                     | 130                      | 0                       |
|      | Nanshen Lake    | 0                              | 165                      | 0                     | 15                       | 0                       |
|      | Xiabeijia       | 0                              | 2                        | 0                     | 0                        | 0                       |
|      | Shangbeijia     | 0                              | 44                       | 0                     | 9                        | 0                       |
|      | Shentangzi Lake | 0                              | 2                        | 0                     | 0                        | 0                       |
|      | Beishen Lake    | 0                              | 25                       | 0                     | 195                      | 0                       |
|      | Total           | 157                            | 289                      | 15                    | 2779                     | 0                       |
| 2016 | Zhanbei Lake    | 0                              | 0                        | 0                     | 8                        | 0                       |
|      | Sanhu Lake      | 0                              | 2                        | 1420                  | 7                        | 0                       |
|      | Changhu Lake    | 0                              | 2                        | 0                     | 0                        | 0                       |
|      | Sanniwan        | 102                            | 0                        | 0                     | 87                       | 0                       |
|      | Baisha Lake 2   | 150                            | 40                       | 800                   | 80                       | 0                       |
|      | Baisha Lake 1   | 0                              | 80                       | 0                     | 0                        | 0                       |
|      | Xiabeijia       | 0                              | 0                        | 0                     | 20                       | 0                       |
|      | Shangbeijia     | 0                              | 0                        | 0                     | 50                       | 0                       |
|      | Total           | 252                            | 124                      | 2220                  | 252                      | 0                       |
| 2017 | Zhanbei Lake    | 80                             | 0                        | 0                     | 31                       | 0                       |
|      | Changhu Lake    | 0                              | 10                       | 0                     | 175                      | 50                      |
|      | Sanniwan        | 4500                           | 0                        | 0                     | 114                      | 0                       |
|      | Baisha Lake 2   | 0                              | 34                       | 0                     | 212                      | 0                       |
|      | Baisha Lake 1   | 0                              | 50                       | 0                     | 600                      | 0                       |
|      | Nanshen Lake    | 0                              | 50                       | 0                     | 0                        | 0                       |
|      | Xiabeijia       | 0                              | 53                       | 0                     | 3                        | 0                       |
|      | Shentangzi Lake | 0                              | 0                        | 0                     | 2                        | 0                       |
|      | Beishen Lake    | 0                              | 0                        | 0                     | 300                      | 0                       |
|      | Total           | 4580                           | 197                      | 0                     | 1437                     | 50                      |
| 2018 | Zhanbei Lake    | 0                              | 5                        | 0                     | 15                       | 0                       |
|      | Sanhu Lake      | 1300                           | 0                        | 0                     | 500                      | 0                       |
|      | Changhu Lake    | 0                              | 0                        | 0                     | 453                      | 0                       |
|      | Fengwei Lake    | 0                              | 0                        | 0                     | 110                      | 0                       |
|      | Sanniwan        | 2199                           | 0                        | 0                     | 12                       | 0                       |
|      | Baisha Lake 1   | 0                              | 10                       | 0                     | 232                      | 0                       |

Table continues on next column.....

| Year | Sample area     | Species                        |                          |                       |                          |                         |
|------|-----------------|--------------------------------|--------------------------|-----------------------|--------------------------|-------------------------|
|      |                 | <i>Recur-virostra avosetta</i> | <i>Vanellus vanellus</i> | <i>Limo-sa limosa</i> | <i>Tringa erythropus</i> | <i>Cal-idris alpina</i> |
|      | Nanshen Lake    | 0                              | 0                        | 0                     | 8                        | 0                       |
|      | Xiabeijia       | 0                              | 180                      | 0                     | 0                        | 0                       |
|      | Shangbeijia     | 50                             | 28                       | 0                     | 0                        | 0                       |
|      | Shangbeijia 2   | 0                              | 0                        | 0                     | 4                        | 0                       |
|      | Shentangzi Lake | 0                              | 2                        | 0                     | 0                        | 0                       |
|      | Beishen Lake    | 1737                           | 9                        | 0                     | 319                      | 0                       |
|      | Total           | 5286                           | 234                      | 0                     | 1653                     | 0                       |
| 2019 | Sanhu Lake      | 400                            | 0                        | 0                     | 600                      | 0                       |
|      | Changhu Lake    | 100                            | 0                        | 0                     | 250                      | 0                       |
|      | Fengwei Lake    | 0                              | 0                        | 0                     | 26                       | 0                       |
|      | Sanniwan        | 912                            | 0                        | 700                   | 101                      | 0                       |
|      | Baisha Lake 1   | 500                            | 0                        | 0                     | 20                       | 0                       |
|      | Nanshen Lake    | 2                              | 73                       | 0                     | 1400                     | 0                       |
|      | Xiabeijia       | 0                              | 40                       | 0                     | 0                        | 0                       |
| 2020 | Shangbeijia     | 4                              | 150                      | 0                     | 80                       | 0                       |
|      | Shentangzi Lake | 170                            | 53                       | 0                     | 250                      | 0                       |
|      | Beishen Lake    | 270                            | 11                       | 0                     | 765                      | 0                       |
|      | Total           | 2358                           | 327                      | 700                   | 3492                     | 0                       |
|      | Changhu Lake    | 0                              | 77                       | 0                     | 420                      | 1530                    |
|      | Fengwei Lake    | 18                             | 30                       | 0                     | 438                      | 0                       |
|      | Sanniwan        | 40                             | 240                      | 0                     | 3                        | 0                       |
|      | Total           | 58                             | 347                      | 0                     | 861                      | 1530                    |

**Table IV. Spatial niche overlap of five dominant shorebirds in Nanji Wetland National Nature Reserve of Poyang Lake.**

| <i>Recurvirostra avosetta</i> | <i>Recur-virostra avosetta</i> | <i>Vanellus vanellus</i> | <i>Li-mosa limosa</i> | <i>Tringa stag-natilis</i> | <i>Cal-idris alpina</i> |
|-------------------------------|--------------------------------|--------------------------|-----------------------|----------------------------|-------------------------|
| <i>Vanellus vanellus</i>      | 0.294                          |                          |                       |                            |                         |
| <i>Limosa limosa</i>          | 0.389                          | 0.234                    |                       |                            |                         |
| <i>Tringa stagnatilis</i>     | 0.412                          | 0.458                    | 0.305                 |                            |                         |
| <i>Calidris alpina</i>        | 0.008                          | 0.069                    | 0.005                 | 0.219                      |                         |

The shorebirds in the East Asian–Australasian flyway mainly breed in Siberia and overwinter in Australia. Most of them migrate through the eastern coastal areas of China, and the number of species resting in inland wetlands of China is small (Chen *et al.*, 2015). However, some shorebirds need to stop in inland wetlands during the migration period, and their population size is large. These



wetlands are indispensable as overwintering or stopover sites. For example, common redshank *Tringa totanus*, Kentish plover, and black-tailed godwit are the main species in Qinghai Lake during overwintering period, and wood sandpiper *Tringa glareola*, Pacific golden plover *Pluvialis fulva*, spotted redshank, and common greenshank *Tringa nebularia* are the main species in the Poyang Lake area (Li *et al.*, 2015; He *et al.*, 2019).

From 2015 to 2020, the number of species (5–7) showed little variation, indicating that the reserve could provide a stable wintering environment for a variety of shorebirds. The species with large population numbers in this survey included spotted redshank and pied avocet, which have become dominant species in some years, as in other areas of Poyang Lake (Zhi *et al.*, 2020). These two species also have large population size and wide distribution range in provinces around Jiangxi Province, such as Anhui (Chen and Zhou, 2011) and Hubei (Zhou *et al.*, 2018). They can become dominant species in other lakes with climate and habitat conditions similar to those of Poyang Lake. The population size of these two species in coastal provinces such as Zhejiang (Jiang *et al.*, 2011) and Fujian (Liu, 2003) is significantly lower than those of black-tailed godwit and dunlin. Therefore, spotted redshank and pied avocet are more suitable for inhabiting inland lakes such as Poyang Lake.

#### *Spatial-temporal distribution and niche separation of the dominant species*

Shorebirds are small and medium-sized birds, and their main diurnal behavior during the overwintering period is foraging and resting (Shen *et al.*, 2016; Chan *et al.*, 2019). Therefore, the main functions of overwintering and resting places for shorebirds are to provide food and resting places.

The habitat utilization and selection of shorebirds is mainly related to their ecological habits, habitat characteristics, and human activities, which affect the population size and spatial distribution of shorebirds (Ge *et al.*, 2006). For example, this survey shows that the shorebird species observed in the largest number of sampled areas in Nanji Wetland National Nature Reserve of Poyang Lake was spotted redshank, which was distributed in all sampled areas. Although the population size of spotted redshank showed drastic fluctuation, its annual distribution in sampled areas was basically stable. They were concentrated in areas such as Sanhu Lake, Changhu Lake, and Nanshen Lake.

These results showed that the adaptability of spotted redshank in Poyang Lake was stronger than that of other shorebirds. Spotted redshank usually gathers in small groups to forage for benthic biota in the shallow water

(Zhao, 2001; Shen *et al.*, 2016). It is also common that hundreds of spotted redshank gather in large groups in Poyang Lake to look for food in shallow water or relatively deeper lake areas, and spotted redshank is better able to adapt to using different levels of water depth than other shorebirds. They often upend while feeding in deep water area, and even swim. Other shorebirds in Poyang Lake cannot swim or do not upend while feeding. Various group sizes, foraging methods, and the ability to use different levels of water depth are important factors that shape the strong adaptability of spotted redshank. Therefore, the distribution range, temporal niche (0.880), and spatial niche (0.798) of spotted redshank are wide.

The population size of pied avocet was also large, but showed the largest fluctuations among the five dominant shorebirds. Pied avocet usually gather in a large group (hundreds or even thousands) to forage in a lake area, but their encounter rate is much lower than those of spotted redshank and Northern lapwing, and they had few cumulative sampled areas. Therefore, the spatial niche of pied avocet was narrower than that of spotted redshank and Northern lapwing.

The temporal niche (0.972) and spatial niche (0.830) of Northern lapwing were the widest. Northern lapwing is an omnivorous bird that forages on small invertebrates, plant leaves, and seeds in mud land, grassland, farmland, and other habitats (Zhao, 2001). Because their food resource is more diverse and suitable habitats can be found in different areas, their population size was more stable than that of other shorebirds, and their temporal and spatial niches were also wider. Northern lapwing usually lives in small groups; therefore, their annual encounter rate was high. However, their population size was much smaller than that of other dominant shorebirds.

Northern lapwing and spotted redshank in Poyang Lake exhibited stronger adaptability and were more widely distributed than other shorebirds. The niche overlap of the two species was the highest in the spatial-temporal dimensions. They had spatial niche separation to decrease competition and improve coexistence, mainly through differences in food composition, foraging mode, and micro-habitat.

Pied avocet was distributed in 11 sampled areas, and their spatial-temporal niche was relatively wide. This is because their foraging habits are similar to that of spotted redshank, and they prefer to forage on benthic biota in shallow water. The body size of pied avocet is obviously larger than that of spotted redshank. Although pied avocet does not have the ability to upend while feeding, its long legs are very beneficial for adapting to different levels of water depth. Therefore, the spatial niche overlap between pied avocet and spotted redshank

was also high, even though the foraging methods of the pied avocet and spotted redshank are different. The pied avocet adopts the strategy of sweeping food in the water with its beak while walking (Zhao, 2001). Pied avocet and spotted redshank often share the same lake area, but they usually forage in separate groups. Therefore, they had spatial niche separation to decrease competition and improve coexistence mainly, through differences in foraging mode and micro-habitat.

This study showed that most shorebirds were concentrated in Zhanbei Lake, Sanhu Lake, Changhu Lake, Sanniwan, and Beishen Lake, with large and stable population sizes. These findings indicate that there are limited places for shorebirds to forage and rest during the overwintering period, and there is great interspecific competition. These sampled areas have more abundant micro-habitat types, especially the shallow water and mud land areas, which can provide habitat for many shorebirds.

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### IRB approval and ethical statement

The study was involved only observation of shorebirds, therefore, IRB approval and ethical statement was not needed.

### Statement of conflict of interest

The authors have declared no conflict of interest.

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