



Full length article

Impacts of prolonged dry season and artificial food supply on the wintering spatial distribution of Siberian Cranes: Implications for conservation

Deming Shen^a, Fawen Qian^b, Shaoxia Xia^c, Chaoyang Wang^a, Xu Chu^d, Zhenyu Wang^a, Hongxing Jiang^{b,*}, Yankuo Li^{a,**}

^a College of Life Sciences, Jiangxi Normal University, Nanchang, 330022, China

^b Key Laboratory of Forest Ecology and Environment of State Forestry Administration Institute of Forestry Ecology, Environment and Protection, Chinese Academy of Forestry, Beijing, 100091, China

^c Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing, 100101, China

^d Shanghai Municipal Engineering Design Institute (Group) CO., LTD., Shanghai, 200082, China

ARTICLE INFO

Keywords:

Artificial habitats
Artificial provisioning
Poyang lake
Prolonged dry season
Siberian crane
Spatial distribution

ABSTRACT

Poyang Lake, China's largest freshwater lake, is a critical wintering ground for most of the global Siberian Crane (*Grus leucogeranus*) population. However, increasingly prolonged dry seasons have degraded the natural wetlands of Poyang Lake, forcing Siberian Cranes to shift to artificial habitats. From 2015 to 2023, field surveys revealed a substantial increase in the number of Siberian Cranes in artificial habitats, with peak counts reaching 3000 individuals, accounting for up to 53% of the species' global population. Satellite telemetry of 13 individuals further confirmed the spatial use of these habitats, highlighting their consistent reliance on artificial sites over multiple years. Seven high-use hotspots were identified outside of Poyang Lake, including two artificial provisioning sites that supported dense foraging flocks for extended periods. Satellite telemetry confirmed this trend, with artificial habitats making up to 64.2% of the occurrence sites in some years. This reliance on artificial habitats was closely linked to the reduced tuber biomass in natural wetlands and low winter water levels in Poyang Lake, which collectively explained 83% of the variance in crane abundance in artificial habitats. Artificial habitat use peaked in December and January, indicating marked seasonal variation. Siberian Cranes also exhibited a pronounced circadian rhythm, foraging in artificial habitats during the day and returning to natural wetlands to roost at night. Despite the shift toward artificial habitats, natural wetlands remain critical for nighttime refuge. The continued dependence on artificial habitats raises concerns about disease transmission owing to dense congregations. Conservation strategies should prioritize both the careful management of artificial provisioning sites and the restoration of natural wetlands to improve food and habitat availability within natural ecosystems, ultimately enabling the return of Siberian Cranes to their traditional natural habitats.

1. Introduction

The Siberian Crane (*Grus leucogeranus*) is a large migratory wading bird with an estimated global population of approximately 5600 individuals (Wen et al., 2023). It is classified as a globally Critically Endangered (CR) species by the International Union for Conservation of Nature. The species is divided into two geographically isolated populations: eastern Asian and western/central Asian populations. In recent years, only one individual from the western/central Asian population

has been recorded wintering along the southern coast of the Caspian Sea in Iran (Mirande and Ilyashenko, 2019). Today, the entire global population of Siberian Cranes is confined to the East Asian group, making its conservation critical. This population breeds in the Arctic tundra of Siberia and migrates to winter at or near Poyang Lake, located in the middle reaches of the Yangtze River Basin in China (Yi et al., 2022).

Poyang Lake, the largest freshwater lake in China, is an important global wintering ground for migratory waterbirds. Over 426,000 waterbirds winter here annually, with numbers peaking at a record

Peer review under the responsibility of Editorial Office of Avian Research.

* Corresponding author.

** Corresponding author.

E-mail addresses: hxjiang@caf.ac.cn (H. Jiang), liyankuo@jxnu.edu.cn (Y. Li).

<https://doi.org/10.1016/j.avrs.2025.100308>

Received 23 March 2025; Received in revised form 30 July 2025; Accepted 22 September 2025

Available online 10 October 2025

2053-7166/© 2025 The Authors. Publishing services by Elsevier B.V. on behalf of KeAi Communications Co. Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

725,760 individuals in one year (Li et al., 2019). Since the 1980s, when Siberian Crane flocks were first documented at Poyang Lake, the wetlands have become crucial habitats for the survival of this critically endangered species (Wu and Ji, 2002; Li et al., 2012a). Extensive research and conservation efforts in the Poyang Lake region have greatly advanced our understanding of the Siberian Crane and have contributed to its population recovery (Li et al., 2012a; Shan et al., 2012; Burnham et al., 2017). Over the past two decades, the collapse of the western/-central Asian population has further underscored the importance of the eastern population wintering at Poyang Lake, which has become the species' final stronghold (Mirande and Ilyashenko, 2019). From a genetic conservation perspective, the eastern population also serves as a critical source for potential gene rescue efforts aimed at the western/-central Asian population (Chen et al., 2025). Consequently, Poyang Lake has emerged as a critical global sanctuary for Siberian Crane conservation.

Over the past two decades, prolonged dry seasons have severely degraded the Siberian Crane habitat at Poyang Lake (Li et al., 2020). Prolonged dry seasons significantly reduce the lake water surface area, thereby diminishing the availability of suitable habitats for Siberian Cranes (Jiang et al., 2014; Zhang et al., 2014). Typically, the water level of Poyang Lake begins to recede in October and enters a dry phase from November to March, which coincides with the overwintering period of Siberian Cranes (Wu and Ji, 2002). This reduction in water coverage exposes extensive mudflats and forms numerous saucer-shaped lakes that provide critical habitats for cranes (Li et al., 2012a). However, since 2003, low autumn water levels and prolonged dry spells have become persistent trends, leading to a substantial decline in potential habitat areas for the Siberian Crane (Li et al., 2023; Xue et al., 2023). During these dry periods, the lake's water surface typically ranges from 618.8 to 2498.7 km², with an average of 1242.0 km² (Sun et al., 2021). In 2022, Poyang Lake experienced an extreme drought, with water levels dropping to their lowest recorded levels since the 1950s (Chen et al., 2023; Zhang et al., 2023). The lake entered a low-water period 105 days earlier than usual, with its surface area shrinking to a mere 226 km² by November 18 (Min et al., 2024).

Moreover, Siberian Cranes in the Poyang Lake wetlands have recently faced severe food shortages. *Vallisneria* plant tubers, which are a critical food source for this species in natural wetlands, have been declining (Jia et al., 2013; Burnham et al., 2017; Hou et al., 2020). Long-term monitoring data from 1999 to 2017 revealed a significant linear decline in tuber density, with levels often dropping to critically low numbers after 2009, averaging approximately one-quarter of the pre-2009 densities (Li et al., 2020). Further monitoring indicated continued deterioration in tuber growth, with densities recorded as zero in 2020, 2021, and 2022 (Xu et al., 2021, 2023, 2024). Tuber biomass followed a parallel decline, mirroring the trend in tuber density from 1999 to 2016 (Hou et al., 2020). This drastic reduction in *Vallisneria* tuber availability has resulted in a persistent food scarcity for overwintering Siberian Cranes at Poyang Lake, which has been significantly correlated with the timing of autumn droughts and summer floods (Li et al., 2020; Hou et al., 2020).

The degradation of overwintering habitats has driven significant adaptive changes in the wintering behavior of Siberian Cranes at Poyang Lake, including shifts in habitat use and dietary composition. This species has increasingly shifted from its preferred shallow-water wetlands and mudflats to grasslands (Jia et al., 2013; Burnham et al., 2017), and more recently, to artificial habitats, such as rice fields and lotus ponds, which have become important foraging areas (Wang et al., 2019). Concurrently, their diet has shifted from *Vallisneria* plant tubers in natural habitats to *Potentilla limprichtii* in meadows and rice and lotus in artificial habitats (Jia et al., 2013; Hou et al., 2021). To mitigate food scarcity, feeding stations have been established in Liyuzhou and Chazhou by volunteers and local forestry departments. These two stations, spanning 50–70 ha, provide wintering food for Siberian Cranes through the cultivation of lotus roots and the maintenance of unharvested rice

fields. These sites support foraging populations of 1000–3000 Siberian Cranes, creating a high-density aggregation that persists for nearly two months (Zhi et al., 2019; Wen et al., 2023).

As prolonged dry seasons become more frequent, the relative importance of natural wetlands and artificial habitats for overwintering Siberian Cranes remains unclear. The response of the spatial use patterns of Siberian Cranes to prolonged dry seasons remains poorly understood. In this study, we monitored Siberian Crane population dynamics in artificial habitats through field surveys from 2015 to 2023, and employed satellite tracking technology to continuously monitor 13 Siberian Cranes from 2018 to 2023 at Poyang Lake. We analyzed their numbers, distribution, and utilization intensity in artificial and natural habitats at Poyang Lake and the relationship between their spatial distribution patterns and prolonged dry seasons. The main objectives of this study were: (1) to assess whether Siberian Cranes have become increasingly reliant on artificial habitats outside Poyang Lake for overwintering, and whether these external habitats have now become primary overwintering grounds; (2) to analyze the annual and monthly variation of artificial habitats utilization by Siberian Cranes, compare the utilization intensity between artificial and natural habitats, and explore the correlation between utilization intensity of artificial habitats and food condition and prolonged dry seasons in Poyang Lake; and (3) to explore whether "artificial feeding sites" established outside Poyang Lake have influenced the distribution patterns of Siberian Cranes, potentially transforming these areas into key activity zones for the species. The findings of this study enhance our understanding of the dynamic spatial distribution patterns of Siberian Cranes during the overwintering period and their relationship with prolonged dry seasons and artificial provisioning, thereby providing valuable scientific insights into crane conservation and habitat restoration.

2. Materials and methods

2.1. Study area

Poyang Lake, located in northern Jiangxi Province, China (28°11' N to 29°51' N, 115°49' E to 116°36' E), encompasses a drainage basin of approximately 162,000 km² (Fig. 1). It is naturally connected to the Yangtze River, and its hydrological regime is primarily governed by the inflow from five major tributaries and outflow into the Yangtze River. However, during summer, river-lake flow reversal may occur when the water level of the Yangtze River exceeds that of Poyang Lake, leading to a backflow into the lake.

Poyang Lake exhibits pronounced seasonal hydrological variations that are characteristic of a seasonal lake, with distinct wet and dry periods. During the wet period (April–October), water levels begin to increase in April, peaking at 18–21 m above mean sea level (m.s.l.) by July, resulting in extensive floodplain inundation exceeding 3000 km² (Shankman et al., 2009). In contrast, during the dry period (November–March), water levels decrease to 9–12 m (m.s.l.), causing a substantial reduction in the lake surface area to less than 1000 km². This contraction leads to the formation of narrow sinuous channels and multiple isolated saucer-shaped sublakes.

Saucer-shaped sublakes are shallow and seasonally inundated sublakes that emerge within Poyang Lake during the dry season. During the wet season, saucer-shaped sublakes merge into the main lake body. As the water level drops below 16.4 m, these sublakes gradually become visible. When it falls to approximately 13.8 m, they become isolated water bodies with no direct hydrological connection to the main lake. A total of 102 saucer-shaped sublakes have been identified within Poyang Lake, covering an area of 816.3 km², which accounts for 22.3% of the total area of Poyang Lake, and have become crucial waterbird wintering grounds, supporting over 80% of the overwintering waterbirds in Poyang Lake (Hu et al., 2015).

The autumn water level recession at Poyang Lake creates extensive wetlands, shallow waters, and grassy marshes, providing an ideal

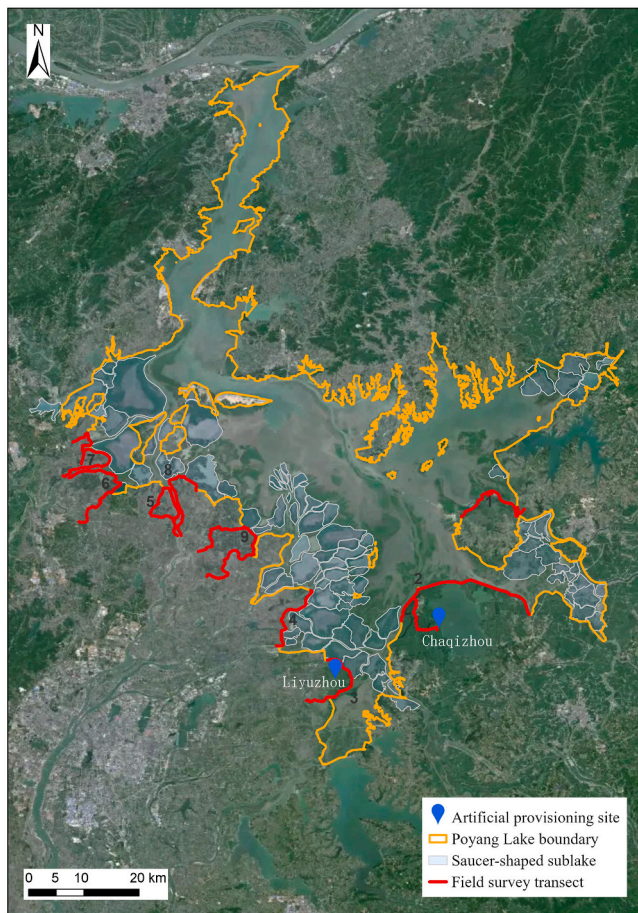


Fig. 1. Study site at Poyang Lake along with survey transects in artificial habitats and artificial provisioning sites. The numbers indicate the transect IDs.

habitat for cranes. The lake supports four wintering crane species, with the critically endangered Siberian Crane being the most prominent. Approximately 86.0% of the global Siberian Crane population winters in Poyang Lake (Wen et al., 2023). In comparison, the White-naped Crane (*Antigone vipio*) and Hooded Crane (*Grus monacha*) maintain wintering populations of approximately 300–1000 individuals in the lake, while the Common Crane (*Grus grus*) averages around 2300 wintering individuals, although the numbers exceeded 8000 some years (Li et al., 2012b). As a globally significant wintering site, the wetland conditions at Poyang Lake are crucial for the recovery of crane populations, particularly the critically endangered Siberian Crane.

2.2. Field survey

To monitor the population of Siberian Cranes in artificial wetlands, such as rice paddies and lotus ponds around Poyang Lake, we established nine fixed survey transects spanning 258 km (Fig. 1). Transects eight and nine were added in 2020 to improve the spatial coverage. To ensure consistency and comparability across years, only data from the original seven transects (established in 2015) were used for the subsequent analyses of population trends and environmental drivers. Surveys were conducted 1–3 times a month between 2015 and 2023. On weekends with favorable weather conditions from October to March each year, the research team, divided into two groups of 3–4 members, conducted field surveys along the transects. Due to access restrictions caused by the COVID-19 outbreak, field surveys during the winter of 2019 were conducted only in November and December, with no data collected from January to March 2020. Upon encountering waterbirds, the team recorded the species, population size, and geographical

coordinates. To ensure data comparability across years and transects, survey methods, including transect design, observation protocols, and data recording procedures, were standardized and maintained throughout the study period. The same core team of trained observers conducted the surveys using consistent equipment, minimizing inter-observer and inter-year variability. Besides the logistical disruptions caused by the COVID-19 pandemic during winter 2019, no major changes in personnel, equipment, or methodology occurred during the course of this study.

To account for the variation in survey frequency across months and enhance interannual comparability, both the annual maximum and mean counts of Siberian Cranes were calculated. Specifically, the annual maximum was defined as the highest value among the monthly maximum counts from November to March, and the annual mean was calculated as the average monthly mean across the same period. Furthermore, considering that crane numbers typically stabilize by December and that the survey effort was most consistent during this month, we calculated the maximum and mean December counts for each year and analyzed them separately to assess temporal trends. These values were then aggregated to facilitate the trend analysis of temporal changes in crane abundance within the artificial habitats over the study period. Linear regression was used to assess whether the Siberian Crane population showed significant temporal variation. To evaluate temporal trends in Siberian Crane abundance within artificial habitats, simple linear regression was performed using four abundance metrics: annual maximum counts, annual mean counts, December maximum counts, and December mean counts. All linear regression analyses were conducted using R 4.4.1 (R Core Team, 2024).

2.3. Bird satellite tracking data

Between 2018 and 2024, satellite telemetry was employed to monitor 13 Siberian Cranes that had sustained injuries in the wild, using satellite transmitters produced by Hunan Global Messenger Technology Co., Ltd. and their associated data acquisition platforms. These individuals were successfully rescued, rehabilitated, fitted with tracking devices, and reintroduced into their natural habitats. The tracking devices were attached to the legs of the cranes. Each device weighed 27 g and was solar powered. The weight of the devices accounted for less than 3% of the cranes' total body mass, ensuring compliance with the ethical and practical guidelines for wildlife tracking.

Satellite tracking enables the continuous monitoring of Siberian Crane movements in the wild, providing data on location coordinates, time, altitude, and activity levels. Because our study focused on the spatial patterns of Siberian Cranes during winter, satellite telemetry data from the winter months (October to March) were specifically analyzed. An overwintering year was defined as the period from October of one year to March of the following year. For example, the wintering year of 2018 refers to the period from October 2018 to March 2019 (winter 2018).

In ArcGIS Pro, the locations of the Siberian Cranes were overlaid with boundary maps of Poyang Lake and its saucer-shaped sublakes to categorize the points either within or outside the sublakes, as well as in habitats beyond Poyang Lake. Vector boundary data for the overall extent of Poyang Lake were obtained from the Jiangxi Provincial Department of Water Resources, whereas the vector boundaries of the 102 saucer-shaped sublakes were provided by the Jiangxi Forestry Bureau. The habitats outside Poyang Lake primarily consist of rice fields, lotus ponds, and artificially regulated aquaculture lakes, which are classified as artificial habitats. Based on this, Siberian Crane habitats around Poyang Lake were classified into the following three categories: (1) natural habitats within the saucer-shaped sublakes of Poyang Lake (NH-in-SSL); (2) natural habitats located outside the saucer-shaped sublakes but still within the Poyang Lake wetland (NH-out-SSL); and (3) artificial habitats located outside the Poyang Lake wetland (AH-out-PYL).

To investigate temporal variations in habitat use by Siberian Cranes both within and outside Poyang Lake, the day was divided into 24 one-hour periods (0–23), with 0 corresponding to 00:00–01:00, 1 to 01:00–02:00, etc., with 23 representing 23:00–00:00. Additionally, time was categorized into two broad periods: daytime (07:00–17:00) and nighttime (18:00–23:00 and 00:00–06:00). The percentage of crane occurrence sites in each period was calculated and visually represented. To assess the differences in habitat use between daytime and nighttime, we applied a one-way analysis of variance (ANOVA) to compare the percentage of Siberian Crane locations outside Poyang Lake between the two periods. This analysis was conducted using the R software, which is consistent with the other statistical procedures used in this study. Prior to ANOVA, assumptions of normality and homoscedasticity were verified using the Shapiro–Wilk and Levene’s tests, respectively.

2.4. Water level and tuber data

Daily water level data were obtained from the Hydrology Bureau of Jiangxi Province and recorded at the Xingzi Hydrological Station (Fig. 2). The monthly average and maximum water levels were calculated from daily records. Simultaneously, tuber density and biomass were monitored from 1999 to 2023 in three saucer-shaped lakes—Dahuchi, Shahu, and Meixihu—by the Poyang Lake National Nature Reserve and the International Crane Foundation (Li et al., 2012a, 2020). These lakes are critical natural habitats for Siberian Cranes within Poyang Lake.

The distribution pattern of Siberian Crane occurrence sites was illustrated using the "Hot Spot Analysis" tool in ArcGIS Pro to identify areas of high crane activity, or hotspots. Utilization intensity was defined as the proportion of occurrence sites within a given category, reflecting the relative degree to which Siberian Cranes used each habitat type, hotspot, or month. ANOVA was used to assess variation in Siberian Crane utilization intensity across habitat types and hotspots, as well as monthly variation within artificial habitats. All variables met the assumptions of normality and homoscedasticity based on Shapiro–Wilk and Levene’s tests.

To investigate the influence of environmental factors, linear regression models (LM) were constructed to examine the relationships between Siberian Crane abundance metrics and key explanatory variables, including tuber density, tuber biomass, and monthly average water levels. Diagnostic checks confirmed normally distributed residuals for all regression models ($P > 0.05$, Shapiro–Wilk test). Model selection was based on Akaike’s Information Criterion with small-sample correction (AICc), and the model with the lowest AICc was selected as optimal. Following Burnham and Anderson (2002), models with $\Delta\text{AICc} < 2$ were considered plausible alternative models only if they exhibited a

statistically significant overall fit and all included predictors passed significance tests. These models were also reported in the regression results table. All statistical analyses and graphical representations were performed using R 4.4.1 and ArcGIS Pro.

3. Results

3.1. Significant increase in Siberian Crane number in artificial habitats

Both the annual maximum ($R^2 = 0.74$, $P = 0.003$) and mean ($R^2 = 0.54$, $P = 0.03$) number of Siberian Cranes in artificial habitats showed statistically significant increasing trends over time. Similarly, the December maximum ($R^2 = 0.62$, $P = 0.011$) and mean ($R^2 = 0.69$, $P = 0.005$) counts also showed significant upward trends, indicating a consistent increase in crane use of artificial habitat during the core wintering period (Fig. 3). Notably, no Siberian Cranes were observed in artificial habitats during the winter of 2018, and seven individuals were recorded in 2019. However, the number of Siberian Cranes in artificial habitats has increased sharply since 2020. The maximum count surged from 234 ± 316 in the winters of 2015–2019 to 3085 ± 347 in the winters of 2020–2023, while the mean count rose from 62 ± 81 to 1456 ± 413 .

3.2. Artificial habitats emerge as Siberian Crane hotspots

Since the winter of 2018, an average of $42.5 \pm 22.0\%$ of Siberian Crane occurrence sites have been recorded outside Poyang Lake each year (Table 1). In the winter of 2018, the species primarily wintered within the Poyang Lake, with only 0.2% of occurrence sites occurring outside the lake. However, this proportion increased significantly to 50.0% in the winter of 2019 and remained above 42.0% in the following years. The highest proportion of sites outside the lake was recorded in 2022 (64.2%), followed by 51.0% in 2023.

Siberian Cranes were widely distributed across artificial habitats outside Poyang Lake, with notable concentrations in the southwestern, southern, and eastern regions (Fig. 4). Heatmap analysis derived from the satellite tracking data revealed significant hotspots at two artificial

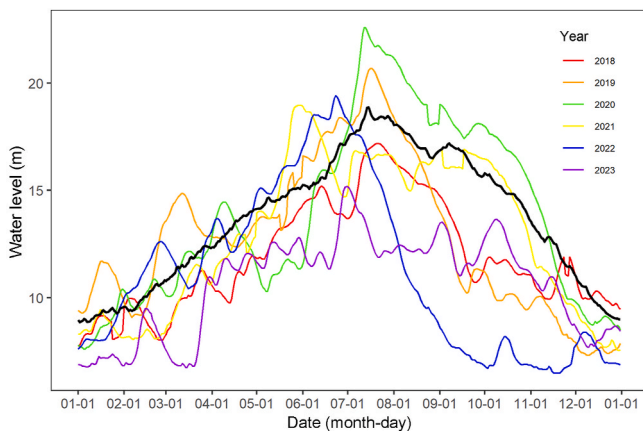


Fig. 2. Daily water levels of Poyang Lake from 2018 to 2023, with the bold black line indicating the median daily water level from 1980 to 2023.

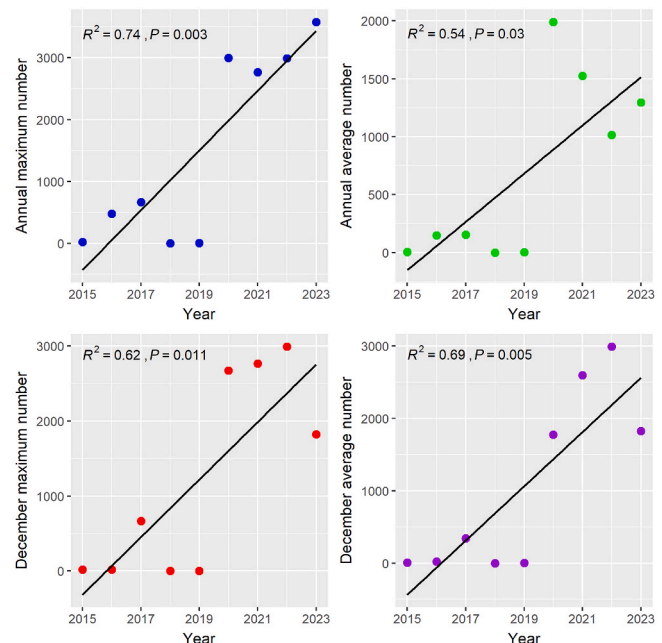


Fig. 3. Temporal trends in annual and December maximum and average numbers of Siberian Cranes recorded in artificial habitats around Poyang Lake (2015–2023). All four abundance metrics exhibited significant increases over the study period.

Table 1
Percentage distribution of Siberian Crane occurrence sites among artificial habitats outside Poyang Lake (AH-out-PYL), natural wetlands within saucer-shaped lakes (NW-in-SSL), and natural wetlands outside saucer-shaped lakes (NW-out-SSL).

Year	AH-out-PYL (%)	NW-in-SSL (%)	NW-out-SSL (%)
2018	0.2	49.6	50.2
2019	50.0	30.5	19.5
2020	47.2	24.8	28.0
2021	42.3	37.7	20.0
2022	64.2	23.7	12.1
2023	51.0	37.1	11.9
Average	42.5	33.9	23.6

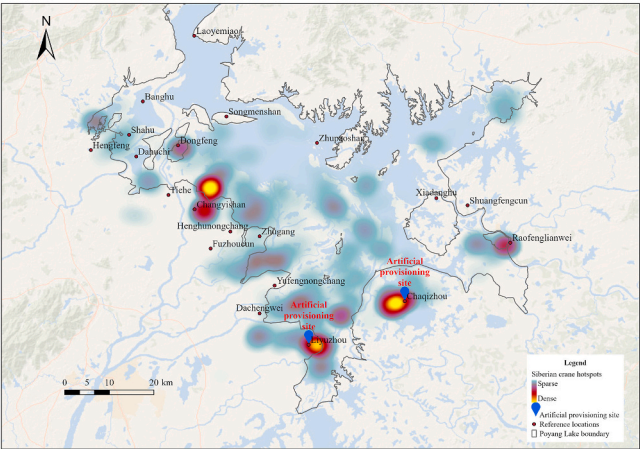


Fig. 4. Siberian Crane activity hotspots derived from satellite tracking locations, showing widespread distribution within and outside Poyang Lake from winter 2019 to winter 2023.

provisioning sites located outside the lake (Fig. 4). From winter 2019 to winter 2023, the annual percentages of crane locations within the Chaqizhou and Liyuzhou artificial provisioning sites were $10.2 \pm 8.6\%$ and $10.2 \pm 12.4\%$, respectively, relative to the total number of locations in artificial habitats. These percentages peaked at 20.3% and 30.4%, respectively. When considering the total winter locations both inside and outside Poyang Lake, the percentages were $4.9 \pm 3.8\%$ and $5.5 \pm 6.5\%$, respectively, with peak values of 9.6% and 15.5%.

A significant hotspot was also identified near Changyishan, where locations in the artificial habitat accounted for $9.6 \pm 3.4\%$ of the total across all artificial habitats, peaking at 13.1%. When considering the total winter locations both inside and outside Poyang Lake, the proportion of locations near Changyishan was $4.8 \pm 1.5\%$, with a maximum of 6.2%. Heatmap analysis of the Siberian Crane observation frequency from field surveys revealed three dense hotspots, including habitats near Changyishan and the artificial provisioning sites at Liyuzhou and Chaqizhou, and four less dense hotspots at Yufengnongchang, Dachengwei, Hongfeng, and Xiadanghu (Fig. 5A). When the heatmap analysis was weighted by the number of Siberian Cranes, only two primary hotspots were identified in the artificial provisioning sites (Fig. 5B). Between 2020 and 2023, 13,578 and 16,413 Siberian Cranes were recorded at the Liyuzhou and Chaqizhou artificial provisioning sites, respectively. The numbers peaked at these sites at 2500 and 3000 individuals, with mean counts of 849 ± 726 and 821 ± 997 per survey, respectively. In contrast, the Changyishan hotspot exhibited a significantly lower crane abundance (37 ± 59 individuals, maximum 257) than both Liyuzhou ($F = 27.42$, $P < 0.001$) and Chaqizhou ($F = 19.87$, $P < 0.001$). However, no significant differences in crane numbers were observed between Liyuzhou and Chaqizhou ($F = 0.142$, $P = 0.709$).

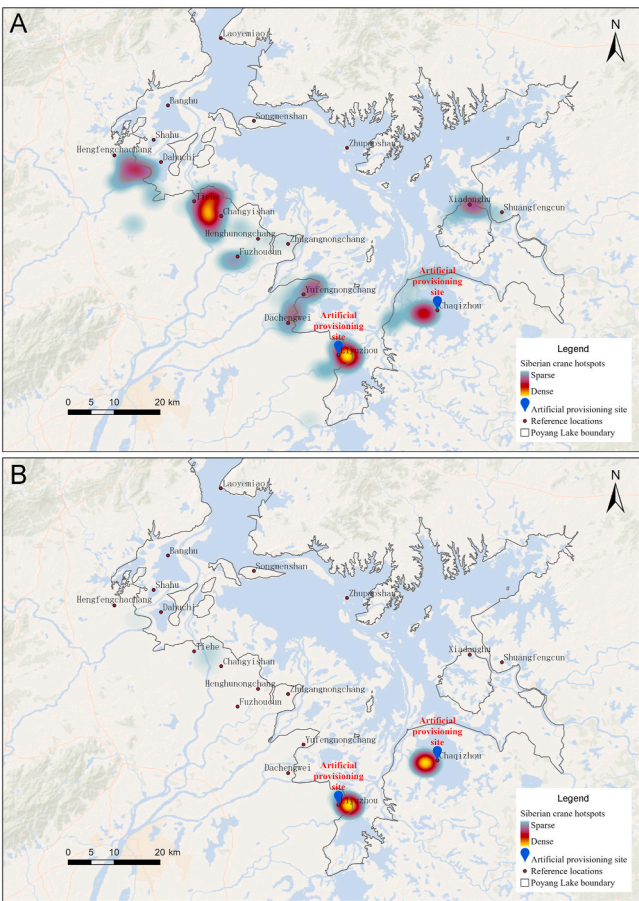


Fig. 5. Siberian Crane hotspots in artificial habitats around Poyang Lake mapped by record frequency (A) and weighted by Siberian Crane numbers (B), highlighting significant hotspots in artificial provisioning sites.

3.3. Monthly and circadian patterns of artificial habitat utilization

The utilization intensity of Siberian Cranes in the artificial habitats of Poyang Lake exhibited distinct monthly variations during the wintering

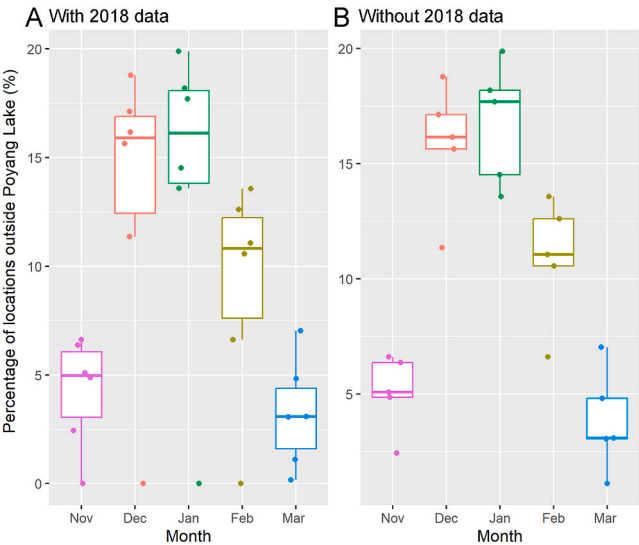


Fig. 6. Proportion of Siberian Crane occurrence sites outside Poyang Lake during the wintering period (with 2018 data (A) and without 2018 data (B)), showing significant monthly variations.

period ($F = 5.31$, $P = 0.003$) (Fig. 6). Upon their arrival in November, $4.2 \pm 2.6\%$ of their occurrence sites (with 2018 data) were located outside the lake. This proportion increased to $13.2 \pm 6.9\%$ in December and $14.0 \pm 7.2\%$ in January, before declining to $9.1 \pm 5.1\%$ in February and further dropping to $3.2 \pm 2.5\%$ in March (Fig. 6A, with 2018 data). Since nearly all occurrence sites were confined to Poyang Lake during the winter of 2018, excluding the 2018 data, the monthly proportions of occurrence sites in artificial habitats followed consistent trends, with peaks in January ($16.8 \pm 2.6\%$) and December ($15.8 \pm 2.8\%$), followed by February ($10.9 \pm 2.7\%$) (Fig. 6B, without 2018 data). The lowest proportions were observed in November ($5.1 \pm 1.7\%$) and March ($3.8 \pm 2.2\%$).

The habitat utilization patterns of Siberian Cranes within and outside of Poyang Lake exhibited a clear circadian rhythm. Specifically, the cranes predominantly foraged outside the lake during the day and roosted inside the lake at night. As shown in Fig. 7, the utilization intensity of artificial habitats remained relatively stable at approximately 40.0% between 6:00 p.m. and 6:00 a.m. but significantly increased to 60.0–70.0% between 8:00 a.m. and 4:00 p.m. In contrast, the utilization intensity of lake wetlands exhibited a marked increase during nighttime hours.

3.4. Interannual variation in artificial habitat use linked to food shortage and prolonged dry season

The abundance of Siberian Cranes in artificial habitats was significantly and negatively correlated with food availability in natural habitats. As shown in Fig. 8, the annual maximum count of Siberian Cranes in artificial habitats was significantly negatively correlated with tuber density ($R^2 = 0.63$, $P = 0.011$) and tuber biomass ($R^2 = 0.64$, $P = 0.01$), whereas the annual average count was also negatively correlated with tuber density ($R^2 = 0.60$, $P = 0.015$) and tuber biomass ($R^2 = 0.61$, $P = 0.013$). Similarly, the December maximum and mean counts were negatively correlated with tuber density ($R^2 = 0.70$, $P = 0.005$; $R^2 = 0.66$, $P = 0.008$) and tuber biomass ($R^2 = 0.69$, $P = 0.006$; $R^2 = 0.65$, $P = 0.009$).

The annual maximum number of Siberian Cranes in artificial habitats was significantly negatively correlated with the January maximum water level ($R^2 = 0.63$, $P = 0.01$), and the December maximum number was also significantly negatively correlated with the January maximum water level ($R^2 = 0.62$, $P = 0.012$) (Fig. 9). The best-fitting linear models (Table 2) indicated that both January maximum water level and tuber biomass were significant negative predictors of the annual maximum number of Siberian Cranes in artificial habitats, jointly explaining 83.0%

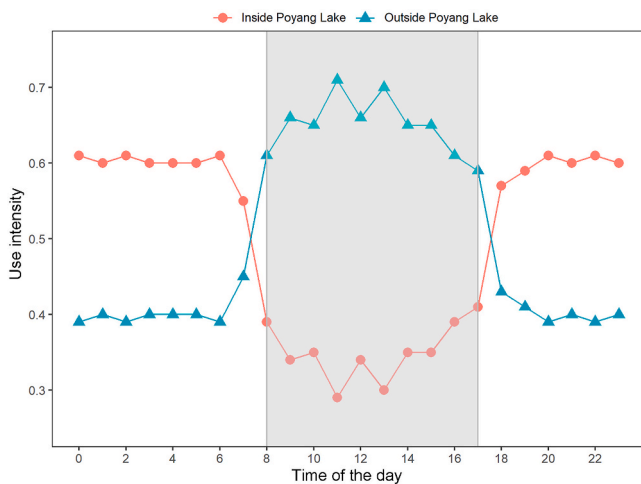


Fig. 7. Temporal variations in the percentage of Siberian Crane locations in habitats inside and outside Poyang Lake, showing a preference for foraging outside the lake during the daytime and roosting inside the lake at night.

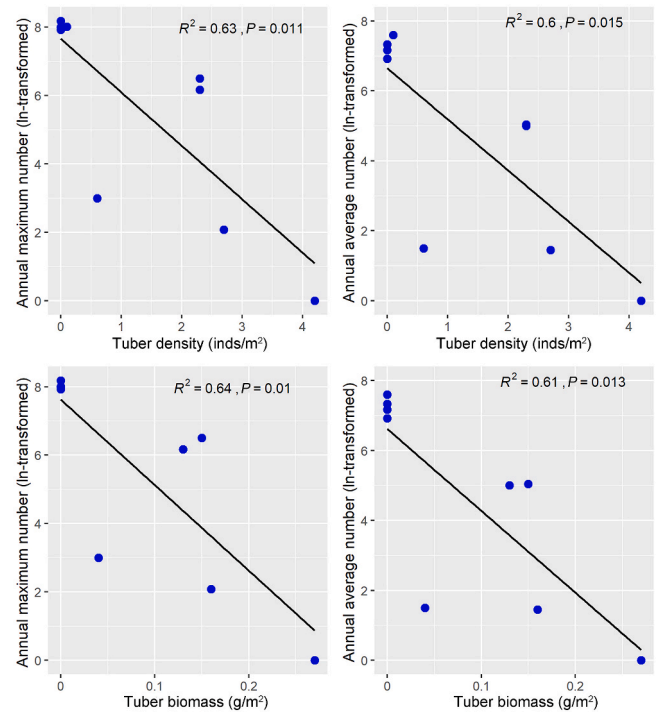


Fig. 8. Maximum and average abundances of Siberian Cranes in artificial habitats showing significant negative correlations with tuber density and biomass.

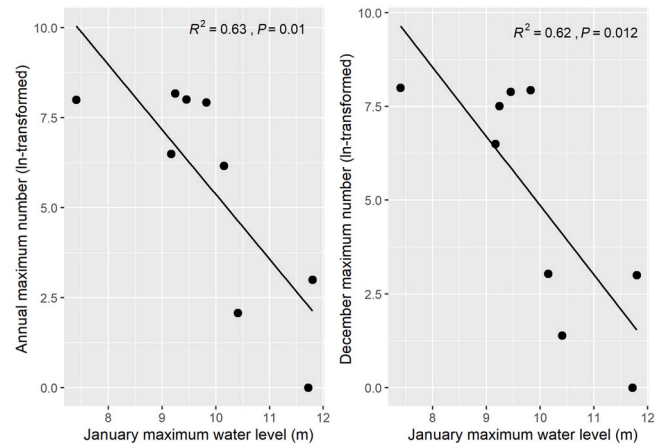


Fig. 9. Significant negative correlations between January maximum water level and the annual maximum number (left) and December maximum number (right) of Siberian Cranes (ln-transformed) in artificial habitats.

of the variance. For the December maximum number, the optimal model included the January maximum water level and tuber density as significant negative predictors, accounting for 87.0% of the variance. In addition to the optimal model, candidate models with $\Delta AICc < 2$ were also considered. These models, which included alternative combinations of tuber biomass and density, demonstrated statistically significant effects for all the included predictors (Table 2). The inclusion of both tuber biomass and density across the models highlighted the consistent negative effects of reduced food availability on crane abundance.

The utilization intensity of Siberian Cranes in artificial habitats was significantly negatively correlated with average water levels in December ($R^2 = 0.71$, $P = 0.036$), January ($R^2 = 0.92$, $P = 0.002$), and March ($R^2 = 0.78$, $P = 0.019$). However, no significant correlations were observed between November ($R^2 = 0.138$, $P = 0.468$) and February (R^2

Table 2

Summary of optimal and candidate linear regression models predicting the (ln-transformed) annual and December maximum numbers of Siberian Cranes in artificial habitats.

	Dependent variable (ln-transformed)	Predictors	Coefficient	t-value	Pr (> t)	Fit	AICc
Optimal	Annual maximum number	Intercept	18.45	4.34	0.005	$R^2 = 0.83$	46.74
		Jan. max. water level	-1.17	-2.58	0.042	$F = 14.58$	
		Tuber biomass	-16.43	-2.64	0.039	$P = 0.005$	
Candidate	Annual maximum number	Intercept	18.61	4.32	0.005	$R^2 = 0.82$	47.05
		Jan. max. water level	-1.18	-2.58	0.042	$F = 13.99$	
		Tuber density	-1.02	-2.55	0.043	$P = 0.006$	
Optimal	December maximum number	Intercept	17.69	4.57	0.004	$R^2 = 0.87$	45.12
		Jan. max. water level	-1.11	-2.71	0.035	$F = 19.47$	
		Tuber density	-1.20	-3.33	0.016	$P = 0.002$	
Candidate	December maximum number	Intercept	17.75	4.34	0.005	$R^2 = 0.85$	46.05
		Jan. max. water level	-1.13	-2.60	0.041	$F = 17.26$	
		Tuber biomass	-18.42	-3.07	0.022	$P = 0.003$	

Both January maximum water level and tuber variables (biomass and density) were included as significant negative predictors in the best-fitting models. Candidate models ($\Delta AICc < 2$) that met significance criteria are also reported.

$= 0.138, P = 0.468$) (Fig. 10).

3.5. Natural wetlands within Poyang Lake remain crucial habitats of Siberian Cranes

As shown in Fig. 4, the heatmap generated from the satellite tracking data of the Siberian Cranes revealed over ten occurrence hotspots distributed across Poyang Lake. From 2018 to 2023, the mean annual percentage of Siberian Crane occurrence sites in natural wetlands within Poyang Lake was $57.5 \pm 22.0\%$, reaching the highest percentage of 99.8% in 2018. Occurrence sites within the saucer-shaped lakes inside Poyang Lake accounted for an average of $33.9 \pm 9.7\%$, while occurrence sites in natural wetlands outside the saucer-shaped lakes were $23.6 \pm 14.3\%$. Because Siberian Cranes were predominantly confined to Poyang Lake in 2018, we compared the percentage of occurrence sites across the

three habitat types from 2019 to 2023 and found significant differences among the three habitat types ($F = 21.35, P < 0.001$) (Fig. 11A). Specifically, the percentage of occurrence sites in habitats within saucer-shaped lakes (NH-in-SSL) was significantly higher than that in habitats outside the saucer-shaped lakes within Poyang Lake (NH-out-SSL) ($F = 8.83, P = 0.018$) but significantly lower than that in artificial habitats outside Poyang Lake ($F = 18.55, P = 0.003$). Furthermore, the percentage of occurrence sites in habitats outside the saucer-shaped lakes within Poyang Lake was significantly lower than in artificial habitats outside Poyang Lake ($F = 42.70, P = 0.000$).

As illustrated in Fig. 11B, the proportions of Siberian Crane locations are ranked as follows: within Poyang Lake during the nighttime ($35.6 \pm 4.0\%$), outside Poyang Lake during the daytime ($27.9 \pm 4.8\%$), outside Poyang Lake during the nighttime ($23.0 \pm 4.2\%$), and within Poyang Lake during the daytime ($13.5 \pm 4.9\%$). Overall, significant differences were observed among the four categories ($F = 4.67, P < 0.05$). Specifically, during the daytime, the proportion of locations outside Poyang Lake was significantly higher than that inside Poyang Lake. Additionally, during the nighttime, the proportion of locations within Poyang Lake was significantly higher than that outside the lake. Furthermore, the proportion of locations inside Poyang Lake during the nighttime was significantly higher than that outside Poyang Lake during the daytime.

4. Discussion

4.1. Artificial habitat utilization

As natural wetlands continue to decline globally, artificial wetlands are becoming increasingly important as essential habitats for waterbirds (Elphick et al., 2010; Ma et al., 2010; Rajpar et al., 2022). This decline is primarily driven by climate change and anthropogenic activities such as dam construction, agriculture, and aquaculture, which have led to the degradation of natural wetland ecosystems (Ma et al., 2019; Rajpar et al., 2022). Consequently, the capacity of these habitats to support waterbird populations has been severely reduced. Researchers and conservationists have increasingly documented the use of artificial habitats by Siberian Cranes, raising significant concerns regarding the ecological implications of this shift (Wang et al., 2019).

This study, based on field monitoring over nine years, revealed a growing dependence of the critically endangered Siberian Crane on artificial habitats around Poyang Lake. The number of Siberian Cranes in artificial habitats showed a significant increasing trend. Specifically, the annual maximum count of Siberian Cranes in artificial habitats rose from fewer than 100 individuals in the winter of 2015 to over 3000 in the winters of 2022 and 2023, representing more than 53% of the global population. Similarly, the average number of cranes in these habitats has increased from fewer than 10 to over 1500, accounting for up to 26.8% of the global population.

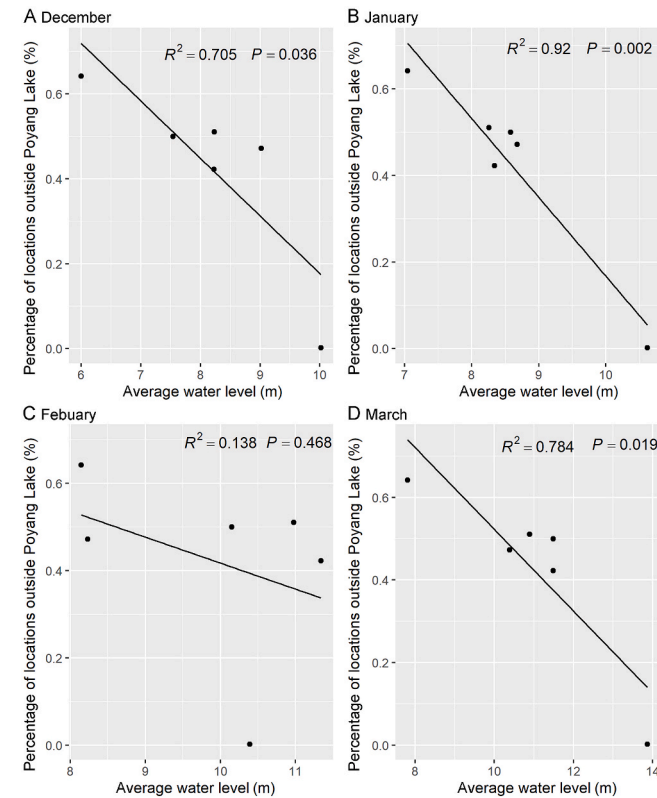


Fig. 10. Percentage of Siberian Crane locations outside Poyang Lake, showing significant negative correlations with average water levels in December (A), January (B), and March (D) but not in February (C).

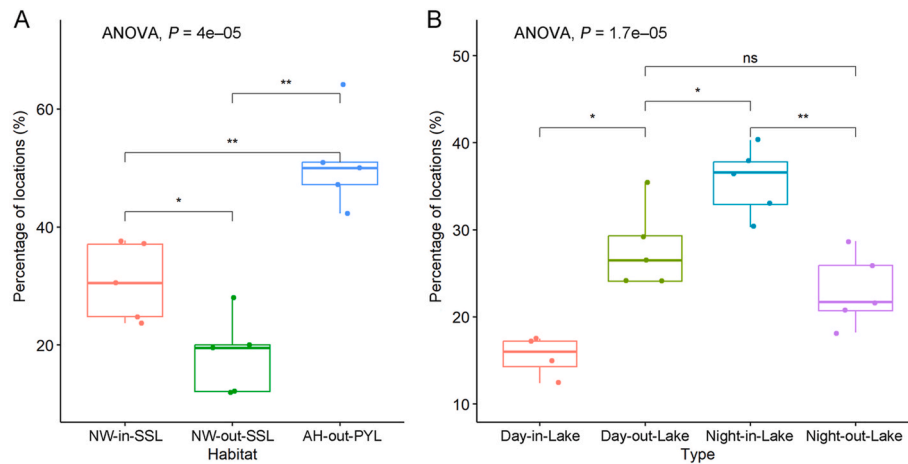


Fig. 11. Distribution of Siberian Crane occurrence locations. (A) Percentages within natural wetlands in saucer-shaped Lakes (NW-in-SSL), natural wetlands outside saucer-shaped lakes (NW-out-SSL), and artificial habitats outside Poyang Lake (AH-out-PYL). (B) Percentages of occurrence inside and outside Poyang Lake during daytime (Day-in-Lake, Day-out-Lake) and nighttime (Night-in-Lake, Night-out-Lake).

Satellite tracking data further underscores the significant reliance of Siberian Cranes on artificial habitats. From winter 2018 to winter 2023, an average of $42.5 \pm 22.0\%$ of Siberian Crane occurrence sites were recorded annually outside Poyang Lake. The winter of 2018 was an exception, with nearly all (98.2%) sites occurring in natural wetlands within Poyang Lake. Excluding 2018, the average annual percentage of occurrence sites outside Poyang Lake increased to $50.9 \pm 8.1\%$, indicating that nearly half of the wintering occurrence sites were in artificial habitats outside Poyang Lake over the past five years. Notably, in the winter of 2022, this percentage peaked at 64.2%. These findings highlight the critical role of artificial habitats in supporting the winter survival of Siberian Cranes.

During the winter of 2019, field surveys recorded fewer than 100 Siberian Cranes, likely underestimating the actual population in artificial habitats owing to restricted access caused by the COVID-19 outbreak between January and March 2020. In contrast, satellite monitoring revealed that 50% of the Siberian Crane occurrence sites during the same period were in artificial habitats outside Poyang Lake, a proportion only surpassed in the winter of 2022 and 2023. This suggests that the population in these habitats was substantially larger than that reported in the ground surveys. This discrepancy highlights the critical need to integrate ground surveys with satellite remote sensing for a more accurate and comprehensive monitoring of Siberian Cranes.

4.2. Drivers of artificial habitat utilization

Waterbird reliance on artificial wetlands is driven by the degradation of natural wetlands (Czech and Parsons, 2002; Sebastián-González et al., 2010). Similarly, our results suggest that the increasing dependence of Siberian Cranes on artificial habitats is a direct result of the ongoing degradation of natural wetlands within Poyang Lake. Our results showed a significant negative correlation between Siberian Crane numbers in artificial habitats and tuber abundance. From 1997 to 2023, the tuber abundance in Poyang Lake steadily declined, with no detection reported in 2022 and 2023 (Li et al., 2020; Xu et al., 2023, 2024). This decline indicates a severe food scarcity for Siberian Cranes within the lake, which corresponds to the increasing reliance of these cranes on artificial wetlands for wintering.

In addition to tuber abundance, we propose that the water level is a critical factor influencing the utilization of artificial habitats by Siberian Cranes. The number of cranes in these habitats was significantly correlated with the average water level in January, whereas the percentage of crane locations in artificial habitats was significantly associated with the average water levels in December, January, and February. We suggest

that winter water levels primarily affect the crane distribution by altering the availability of natural wetland habitats. The prolonged dry season and extremely low water levels in Poyang Lake have led to significant habitat loss in natural wetlands. Over the past 20 years, the duration of the dry season (defined by lake levels <12 m) in Poyang Lake has increased by 39.5% compared to the period from 1953 to 2002 (Xue et al., 2023). This trend has led to prolonged dry seasons and low winter water levels, which are the new normal for the lake. Siberian Crane habitats, particularly mudflats and shallow waters, are typically most extensive when water levels range from 11 to 13 m, with an optimal habitat size of approximately 12 m (Xia et al., 2010; Jiang et al., 2014; Hu et al., 2022). The average water levels in November, December, and January during the winters of 1980–2003 were 12.3 m, 10.9 m, and 9.5 m, respectively, providing extensive suitable habitats for Siberian Cranes. In contrast, during winter from 2015 to 2023, the water levels declined to an average of 10.6 m in November, 9.1 m in December, and 9.0 m in January. According to the habitat suitability model proposed by Hu et al. (2022), water level conditions from 2015 to 2023 led to reductions in suitable habitat areas by 24.7% in October, 20.7% in November, and 8.2% in January relative to the baseline period of 1980–2003. Notably, when the same model was applied to the extremely low water levels recorded in the winter of 2022, the estimated habitat loss increased substantially, reaching 36.5% in October, 60.7% in November, and 39.0% in January. The maximum water level in January and tuber biomass accounted for 83.0% of the variance in the maximum number of cranes in artificial habitats. This underscores the growing reliance of Siberian Cranes on artificial wetlands because of diminishing natural habitat availability.

Food scarcity and habitat loss are not isolated factors. Their combined effects substantially exacerbate the degradation of Siberian Crane wintering habitats, with the cumulative impact being more pronounced than that of either factor alone. Food shortages and habitat loss are significantly correlated with prolonged dry seasons in Poyang Lake. Autumn is a critical period for *Vallisneria* plants, as it produces fully mature seeds and forms tubers (Xiong and Li, 2000). A shorter inundation period in autumn can lead to a significant reduction in tuber biomass (Fox et al., 2014). In addition, larger tubers have been shown to exhibit better survival and growth than smaller tubers (Doyle and Smart, 2001). Therefore, maintaining moderately high water levels in autumn can benefit *Vallisneria* species by promoting tuber production and increasing tuber size. Li et al. (2020) demonstrated that the average water level in October had a significant positive effect on tuber density in the following year, suggesting that higher autumn water levels extend the growing season for submerged plants, enhance biomass

accumulation, and contribute to the establishment of future populations of these plants. The relationship between habitat area and water level has been well documented but has not been addressed further. Nonetheless, the combined effects of food scarcity and habitat loss, driven by changing water levels, highlight the pressing need for comprehensive management strategies to mitigate these challenges and support the survival of wintering Siberian Cranes.

4.3. Risk of artificial habitat utilization

Artificial habitats often function as alternative foraging grounds for waterbirds (Rajpar et al., 2022). In the present study, we found that artificial habitats around Poyang Lake serve as important foraging sites for Siberian Cranes, with cranes foraging in rice fields and lotus ponds during the day and roosting in natural wetlands at night (Fig. 8). As alternative habitats, artificial environments, particularly feeding sites, provide reliable food resources that partially mitigate the effects of natural wetland degradation. These artificial habitats help alleviate the impacts of adverse environmental conditions, delivering critical short-term conservation benefits that enhance the overwinter survival of Siberian Cranes during harsh winters. Artificial provisioning sites are powerful tools for public engagement in conservation. Managed feeding programs create accessible wildlife-viewing opportunities that foster environmental awareness, strengthen community stewardship, and generate ecotourism revenue, all of which are essential for sustaining long-term conservation initiatives in Poyang Lake. Simultaneously, the sites reduce the reliance of cranes on other human-modified habitats, such as agricultural areas, minimize agricultural damage, and foster greater local support for crane conservation.

However, the high-density aggregation of Siberian Cranes at the two artificial feeding sites presents a significant risk of disease transmission. The artificial provisioning sites encompassed approximately 70 ha in Liyuzhou and 60 ha in Chaqizhou. Siberian Cranes formed dense flocks at each site, often numbering between 1000 and 3000 individuals, foraging within a confined area of approximately 20 ha, such as a single rice field or a lotus pond. This high-density foraging behavior typically persists for approximately two months. Such high-density aggregates, particularly those under prolonged exposure, are associated with an elevated risk of disease transmission, including avian influenza (Fu et al., 2020; Wang et al., 2023).

The traditional practice of free-range duck farming in the rice fields surrounding Poyang Lake, combined with the frequent presence of Siberian Cranes in these agricultural areas, increases the likelihood of interactions between wild cranes and domestic poultry, further exacerbating the risk of disease transmission (Wang et al., 2023). Given the critically endangered status of the Siberian Crane and its small global population, the congregation of up to 3000 individuals at a single feeding site poses a significant threat in the event of a disease outbreak, which could have catastrophic consequences. Excessive reliance on artificial feeding may weaken the natural foraging abilities of cranes and reduce their adaptability to fluctuating environmental conditions (Fu et al., 2020). These concerns highlight the urgent need for improved management protocols and rigorous disease monitoring in artificial feeding sites.

4.4. Natural habitat utilization

Before 2012, the Siberian Crane exclusively wintered in the natural wetlands of Poyang Lake, with the Poyang Lake National Nature Reserve serving as its core habitat (Kanai et al., 2002; Li et al., 2012a). The highest recorded count reached 2958 individuals when the global population was estimated to be approximately 3000 (Wu and Ji, 2002). Key wintering habitats within the reserve include saucer-shaped lakes, such as Dahuchi, Shanhu, Banghu, Meixihu, and Dachahu (Shan et al., 2012). In the winter of 1995, satellite telemetry tracking of six Siberian Cranes indicated that their occurrence sites were entirely confined to the

natural wetlands of Poyang Lake, during both the day and night (Li et al., 2012a). Notably, no Siberian Cranes were recorded in artificial habitats until the winter of 2011 (Wang et al., 2019).

Although both field surveys and satellite tracking data have indicated that Siberian Cranes have extensively utilized artificial habitats outside Poyang Lake over the past decade, natural habitats remain essential for their survival. Overall, 49.1% of the recorded occurrence sites were within Poyang Lake, including 13.5% during the day and 35.6% at night. The proportion of crane locations inside Poyang Lake was significantly higher at night than during the day. Additionally, there was a significant increase in the proportion of night-time locations within Poyang Lake, whereas daytime locations within the lake decreased (Fig. 6). These findings suggest that natural wetlands continue to serve as crucial resting habitats for Siberian Cranes and as food resources.

The winter of 2018 was an exception, as all Siberian Cranes overwintered exclusively in the natural wetlands. In winter 2018, particularly in November and December, water levels were close to or slightly higher than the 1980–2003 median, creating favorable conditions for maintaining extensive suitable habitats for Siberian Cranes. Additionally, summer water levels averaged below 17.5 m, which is lower than the historical median, promoting the growth of submerged vegetation and increasing food availability (Li et al., 2020). These optimal environmental conditions underscore the strong preference of cranes for natural wetlands when the habitat quality and food resources are sufficient, thereby relegating artificial wetlands to a supplementary role.

4.5. Conservation implications

As prolonged dry seasons and artificial provisioning have become the prevailing norm in Poyang Lake, an increasing number of Siberian Cranes are expected to rely on the surrounding artificial habitats. A scientifically informed food supply strategy for these artificial habitats is essential to balance emergency food provisioning with the mitigation of disease risks associated with high-density congregations. Establishing multiple spatially dispersed food reserves, such as unharvested rice fields, would ensure a more evenly distributed food supply, reducing reliance on and overcrowding at individual feeding sites, particularly during years of severe wetland degradation. Ultimately, the primary objective is to restore and enhance the natural wetland habitat quality to encourage the return of Siberian Cranes. The key strategies include reinforcing water retention in saucer-shaped lakes by restoring embankments and water control structures. During drought years, water gates should be closed in late summer and early autumn to maximize water storage, followed by a science-based water-level regulation strategy that gradually lowers water levels after the arrival of cranes to ensure optimal wintering conditions.

5. Conclusions

From 2015 to 2023, field surveys and satellite telemetry jointly revealed a substantial increase in Siberian Crane numbers utilizing artificial habitats around Poyang Lake, with peak counts (more than 3000 individuals) exceeding 53% of the species' global population. Key provisioning sites, such as Chaqizhou and Liyuzhou, supported persistent high-density foraging flocks for nearly two months, raising disease transmission concerns. The intensity of artificial habitat use was strongly negatively correlated with tuber abundance and winter water levels in Poyang Lake, with these factors collectively explaining 83.0% of the variation in crane numbers. In years with favorable hydrological conditions (e.g., 2018), cranes reverted to natural wetlands, underscoring the role of food availability and habitat conditions as primary drivers. Despite the heavy daytime use of artificial habitats, natural wetlands remain essential for night-time roosting, reflecting a clear circadian rhythm. In light of the prolonged dry seasons, conservation strategies must simultaneously enhance the management of artificial

habitats and prioritize the restoration of natural wetlands to promote the return of Siberian Cranes to their traditional natural habitats.

CRedit authorship contribution statement

Deming Shen: Writing – original draft, Software, Investigation, Conceptualization. **Fawen Qian:** Methodology, Data curation. **Shaoxia Xia:** Methodology, Investigation. **Chaoyang Wang:** Visualization, Software, Methodology, Investigation. **Xu Chu:** Data curation. **Zhenyu Wang:** Software, Methodology, Investigation. **Hongxing Jiang:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition. **Yankuo Li:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Formal analysis, Conceptualization.

Funding

This study was supported by the National Natural Science Foundation of China (No.32260275) and Fundamental Research Funds of CAF (CAFYBB2024ZA033).

Declaration of competing interest

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

Acknowledgments

We acknowledge Dr. Fengshan Li for his contributions to the design of the field monitoring protocol and thank the Crane Foundation for financial support.

References

- Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second ed. Springer, New York, NY.
- Burnham, J., Barzen, J.E.B., Pidgeon, A.M., Sun, B., Wu, J., Liu, G., et al., 2017. Novel foraging by wintering Siberian cranes *Leucogeranus leucogeranus* at China's Poyang Lake indicates broader changes in the ecosystem and raises new challenges for a critically endangered species. *Bird. Conserv. Int.* 27, 204–223.
- Chen, J., Li, Y., Shu, L., Fang, S., Yao, J., Cao, S., et al., 2023. The influence of the 2022 extreme drought on groundwater hydrodynamics in the floodplain wetland of Poyang Lake using a modeling assessment. *J. Hydrol.* 626, 130194.
- Chen, Q., Lin, H., Zheng, C., Mudrik, E.A., Kashentseva, T.A., Cheng, Y., et al., 2025. Understanding the past to preserve the future: genomic insights into the conservation management of a critically endangered waterbird. *Mol. Ecol.* 34, e17606.
- Czech, H.A., Parsons, K.C., 2002. Agricultural wetlands and waterbirds: a review. *Waterbirds* 25, 56–65.
- Doyle, R.D., Smart, R.M., 2001. Impacts of water column turbidity on the survival and growth of *Vallisneria americana* winter buds and seedlings. *Lake Reserv. Manag.* 17, 17e28.
- Elphick, C.S., Parsons, K.C., Fasola, M., Mugica, L., 2010. Ecology and conservation of birds in rice fields: a global view. *Waterbirds* 33, 244.
- Fox, A.D., Meng, F., Liu, J., Yang, W., Shan, K., Cao, L., 2014. Effects of the length of inundation periods on investment in tuber biomass and sexual reproduction by *Vallisneria spirulosa* S.Z. Yan Ramets. *Knowl. Manag. Aquat. Ecosyst.* 414, 3.
- Fu, X., Xiang, X., Dong, Y., Cheng, L., Zhou, L., 2020. Comparing the intestinal bacterial communities of sympatric wintering Hooded Crane (*Grus monacha*) and Domestic Goose (*Anser anser domesticus*). *Avian Res.* 11, 13.
- Hou, J., Liu, Y., Fraser, J.D., Li, L., Zhao, B., Lan, Z., et al., 2020. Drivers of a habitat shift by critically endangered Siberian cranes: evidence from long-term data. *Ecol. Evol.* 10, 11055–11068.
- Hou, J., Li, L., Wang, Y., Wang, W., Zhan, H., Dai, N., et al., 2021. Influences of submerged plant collapse on diet composition, breadth, and overlap among four crane species at Poyang Lake, China. *Front. Zool.* 18, 24.
- Hu, B., Zou, L., Qi, S., Yin, Q., Luo, J., Zuo, L., et al., 2022. Evaluating the vulnerability of Siberian crane habitats and the influences of water level intervals in Poyang Lake wetland, China. *Remote Sens.* 14, 2774.
- Hu, Z., Zhang, Z., Liu, Y., Ji, W., Ge, G., 2015. The function and significance of the shallow-lakes in the Poyang Lake wetland ecosystem. *Jiangxi Hydr. Sci. Technol.* 41, 317–323.
- Jia, Y., Jiao, S., Zhang, Y., Zhou, Y., Lei, G., Liu, G., 2013. Diet shift and its impact on foraging behavior of Siberian crane (*Grus leucogeranus*) in Poyang Lake. *PLoS One* 8, e65843.
- Jiang, F., Qi, S., Liao, F., Ding, M., Wang, Y., 2014. Vulnerability of Siberian crane habitat to water level in Poyang Lake wetland, China. *GIScience Remote Sens.* 51, 662–676.
- Kanai, Y., Ueta, M., Germogenov, N., Nagendran, M., Mita, N., Higuchi, H., 2002. Migration routes and important resting areas of Siberian cranes (*Grus leucogeranus*) between northeastern Siberia and China as revealed by satellite tracking. *Biol. Conserv.* 106, 339–346.
- Li, B., Yang, G., Wan, R., 2023. Reassessment of the declines in the largest freshwater lake in China (Poyang Lake): uneven trends, risks and underlying causes. *J. Environ. Manag.* 342, 118157.
- Li, F., Liu, G., Wu, J., Zeng, N., Harris, J., Jin, J., 2012a. Ecological Study of Wetlands and Waterbirds at Poyang Lake. Popular Science Press, Beijing.
- Li, F., Wu, J., Harris, J., Burnham, J., 2012b. Number and distribution of cranes wintering at Poyang Lake, China during 2011–2012. *Chinese Birds* 3, 180–190.
- Li, Y., Qian, F., Silbernagel, J., Larson, H., 2019. Community structure, abundance variation and population trends of waterbirds in relation to water level fluctuation in Poyang Lake. *J. Great Lake. Res.* 45, 976–985.
- Li, Y., Zhong, Y., Shao, R., Yan, C., Jin, J., Shan, J., et al., 2020. Modified hydrological regime from the Three Gorges Dam increases the risk of food shortages for wintering waterbirds in Poyang Lake. *Global. Ecol. Conserv.* 24, e01286.
- Ma, T., Li, X., Bai, J., Cui, B., 2019. Habitat modification in relation to coastal reclamation and its impacts on waterbirds along China's coast. *Global. Ecol. Conserv.* 17, e00585.
- Ma, Z., Cai, Y., Li, B., Chen, J., 2010. Managing wetland habitats for waterbirds: an international perspective. *Wetlands* 30, 15–27.
- Min, J., Yu, J., Zhang, Y., Li, D., Que, J., Tian, Z., et al., 2024. Distribution risks and protection countermeasures of Yangtze finless porpoise in Poyang Lake during abnormal dry period. *Acta Hydrobiol. Sin.* 48, 1642–1650.
- Mirande, C.M., Ilyashenko, E.I., 2019. Crane conservation strategy. Species Review: Siberian Crane (*Leucogeranus leucogeranus*). International Crane Foundation, Baraboo, Wisconsin, USA.
- R Core Team, 2024. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Rajpar, M.N., Ahmad, S., Zakaria, M., Ahmad, A., Guo, X., Nabi, G., et al., 2022. Artificial wetlands as alternative habitat for a wide range of waterbird species. *Ecol. Indic.* 138, 108855.
- Shan, J., Ma, J., Li, Y., Qian, F., Tu, X., 2012. Population and distribution of the Siberian crane (*Grus leucogeranus*) wintering in the Poyang lakes over the past decade. *Zool. Res.* 33, 355–361.
- Shankman, D., Davis, L., De Leeuw, J., 2009. River management, land use change, and future flood risk in China's Poyang Lake region. *Int. J. River Basin Manag.* 7, 423e431.
- Sebastián-González, E., Sánchez-Zapata, J.A., Botella, F., 2010. Agricultural ponds as alternative habitat for waterbirds: spatial and temporal patterns of abundance and management strategies. *Eur. J. Wildl. Res.* 56, 11–20.
- Sun, F., Ma, R., Liu, C., He, B., 2021. Comparison of the hydrological dynamics of Poyang Lake in the wet and dry seasons. *Remote Sens.* 13, 985.
- Wang, W., Wang, L., Hou, J., 2019. Man-made habitats have become important foraging areas of Siberian cranes. *Chin. J. Wildl.* 40, 133–137.
- Wang, W., Wang, Y., Chen, Q., Ding, H., 2023. Effects of diet shift on the gut microbiota of the critically endangered Siberian Crane. *Avian Res.* 14, 100108.
- Wen, L., Wang, L., Ding, H., Li, J., Guo, Y., 2023. Using unmanned aerial vehicle for a population and wintering distribution survey of Siberian crane (*Leucogeranus leucogeranus*). *Acta Ecol. Sin.* 43, 7693–7700.
- Wu, Y., Ji, W., 2002. Study on Jiangxi Poyang Lake National Nature Reserve. China Forestry Publishing House, Beijing.
- Xia, S., Yu, X., Fan, N., 2010. The wintering habitats of migrant birds and their relationship with water level in Poyang Lake, China. *Resour. Sci.* 32, 2072–2078.
- Xiong, B.H., Li, W., 2000. Ecological studies on *Vallisneria L.* in China. *Plant Sci. J.* 18, 500–508.
- Xu, Z., Liu, G., Gong, L., 2021. 2020–2021 Monitoring Report on Natural Resources of Jiangxi Poyang Lake National Nature Reserve. Jiangxi Science and Technology Press, Nanchang.
- Xu, Z., Liu, G., Gong, L., 2023. 2021–2022 Monitoring Report on Natural Resources of Jiangxi Poyang Lake National Nature Reserve. Jiangxi Science and Technology Press, Nanchang.
- Xu, Z., Gong, L., Zhang, H., 2024. 2022–2023 Monitoring Report on Natural Resources of Jiangxi Poyang Lake National Nature Reserve. Jiangxi Science and Technology Press, Nanchang.
- Xue, C., Zhang, Q., Jia, Y., Yuan, S., 2023. Intensifying drought of Poyang Lake and potential recovery approaches in the dammed middle Yangtze River catchment. *J. Hydrol.* 50, 101548.
- Yi, K., Zhang, J., Batbayar, N., Higuchi, H., Natsagdorj, T., Byskatova, I.P., 2022. Using tracking data to identify gaps in knowledge and conservation of the critically endangered Siberian crane (*Leucogeranus leucogeranus*). *Remote Sens.* 14, 5101.
- Zhang, Q., Xue, C., Xia, J., 2023. Impacts, contributing factors and countermeasures of extreme droughts in Poyang Lake. *Bull. Chin. Acad. Sci.* 38, 1894–1902.
- Zhang, Q., Ye, X., Werner, A., Li, Y., Yao, J., Li, X., et al., 2014. An investigation of enhanced recessions in Poyang Lake: comparison of Yangtze River and local catchment impacts. *J. Hydrol.* 517, 425–434.
- Zhi, Y., Lu, P., Dai, N., Shao, M., Zeng, J., 2019. Foraging behaviour of Siberian cranes in lotus pond habitats surrounding Poyang Lake. *Acta Ecol. Sin.* 39, 4266–4272.