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Habitat Quality and Social Behavioral Association Network in a Wintering Waterbirds Community

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Abstract: Migratory waterbirds concentrated in freshwater ecosystems in mosaic environments rely on quality habitats for overwintering. At West Dongting Lake National Nature Reserve (WDLNNR), China, land-use change and hydrology alternation are compounding factors that have affected important wintering areas for migratory waterbirds. Presently, changes in the hydrology and landscape have reshaped natural wintering habitats and their availability, though the impact of hydrological management on habitat selection of wintering waterbirds is largely unknown. In this study, we classified differentially managed habitats and calculated their area using the normalized difference vegetation index (NDVI) to evaluate suitable habitat availability over the study period (2016–2017 and 2017–2018 wintering periods). We then used social behavioral association network (SBAN) model to compare habitat quality through species-species social interactions and species-habitat associations in lakes with different hydrological management. The results indicated that social interactions between and within species structured wintering waterbirds communities, which could be dominated by one or more species, while dominant species control the activities of other co-existing species. Analysis of variance (ANOVA) tests indicated significant differences in SBAN metrics between lakes ($p = 0.0237$) and habitat ($p < 0.0001$) levels. Specifically, lakes with managed hydrology were preferred by more species. The managed lakes had better habitat quality in terms of significantly higher habitat areas ($p < 0.0001$) and lower habitat transitions ($p = 0.0113$). Collectively, our findings suggest that proper hydrological management can provide continuous availability of quality habitats, especially mudflats and shallow waters, for a stable SBAN to ensure a wintering waterbirds community with more sympatric species in a dynamic environment.

Keywords: wintering waterbirds; hydrology; social behavioral association network; habitat quality; habitat availability

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1. Introduction

Variations in animal behavior and resource use in shared environments are identifying factors for understanding habitat suitability, community dynamics and animal interactions. In mixed species groups (MSGs), behavioral interaction networks can identify this variation to address habitat quality. Animals make decisions on habitat choices and resource use through behavioral communication, shared intentionally or unintentionally by other animals in the neighborhood. This continuously produced social information offers rich insight on the fitness and availability state of all the resources needed by co-existing animals in environments that animals select or occupy [1–4]. Despite its established fitness consequences on habitat ecology and resource dynamics, the use of such social information on community dynamics in varying environments remains poorly understood [5–8]. However, because social information is continuously produced, making use of it improves the ability to understand how animals make decisions to perceive and respond to environmental gradients [9] or threats [10].

Animals often use social information to acquire resources; for example, species or groups foraging in a location alert others to food [11] and to perceive and avoid competition [8,12]. Behavioral ecologists have been studying how social information shared between co-existing species turns into associations and can influence habitat selection and use. Behavioral communication can lead to inter- and intra-specific interactions [13–15]. These interactions among species can influence community assembly [16,17], alter ecosystem function and services [18–21]; hence, parameters describing species associations have become a bioindicator of ecosystem health, offering evaluations for success or failure of restoration and/or management treatments [8,13,14,19,22,23]. Species associations arise with repeated interactions between species and can be used to probe what are the consequences of these preferred interactions (e.g., community structure and resource use), and whether these patterns of associations create MSGs interaction networks [24–26].

MSGs represent a non-trophic social behavioral association network (SBAN) in varying environments [8]. Investigations of species association networks in varying environmental gradients are rare in animal MSGs, especially in migratory waterbirds. An important aspect of these species associations is how similar the networks are that they form in different environmental or land-uses conditions [27,28]. Recent application of network analysis to analyze species associations in MSGs offers evaluations for habitat suitability and habitat quality [8,13,19,29–33]. Behavioral network analysis: (1) allows comparisons of the habitat quality of targeted and reference sites that have fitness consequences for organisms [8,34,35]; (2) provides invaluable information about reasons for differences in species behavioral network structures [16,36]; (3) identifies critical resources (food and roosting sites) that make a site suitable or not through species-habitat associations [37]; and (4) provides information on the mechanisms through which species contribute to ecosystem functioning [18,21,38,39].

In wintering migratory waterbirds MSGs, two key behavioral domains (i.e., foraging and roosting) are dramatically influenced by anthropogenic alternation to landscape and hydrology. Landscape of wetland system structures habitat types [40] while fluctuation in hydrology determines the availability of these habitats for selection, resource exploitation and use [41]. Two other behaviors (aggression and competition) that drive sociality are central to community structure and community activity persistence in shared environments [8,29,42]. These antagonistic social behaviors play a pivotal role in communication between species [15,43]. This behavioral communication, if converted into network of connected nodes, offers insights on species-species and species-habitat associations [8]. Understanding the linkages of these associations with management aspects of the ecosystem gives invaluable information on available habitat quality and provides insights on community dynamics in shared environments [44–46].

West Dongting Lake National Nature Reserve (WDLNNR) in China is traditionally a key wintering ground for migratory waterbirds in the East Asian-Australasian Flyway [47]. However, the rapid land cover changes [48] and dramatic hydrological alternations [49] have threatened the conservation status of the lake for migratory waterbirds [50]. The decline in waterbirds population in recent years has prompted national conservation efforts to restore the Ramsar site [51] through hydrological control such as embankments. However, the effects of hydrological management on habitat selection of wintering waterbirds are largely unknown. In a previous study, we constructed social behavioral association networks (SBAN) of MSG in two managed (R1) and two unmanaged (R2) sub-lakes in WDLNNR using time series activity-based abundance data [8]. In this study, we aimed to explore how habitat quality influences the key aspects of these networks. Utilizing remotely sensed time series imagery in Google Earth Engine (GEE) and ArcGIS, we classified habitats using NDVI (the normalized difference vegetation index) and assessed their availability and transition in the sub-lakes. Key SBAN metrics i.e., number of nodes, number of edges, edge density, species interaction preferences (SIP) and behavior interaction preferences (BIP) were then used to compare habitat quality in an attempt to assess the success or failure of management treatments.

2. Materials and Methods

2.1. Study Area

West Dongting Lake National Nature Reserve (WDLNNR: 28°48′–29°07′ N, 111°57′–112°19′ E) is a Ramsar site and an important wintering ground for many migratory waterbird species in the East Asia Austrasia Flyway (EAAF). The lake comprises a seasonally flooded semi-mountainous flat landscape covering a 35,000 ha area, with a variety of sub-lakes being principally managed by controlling the hydrology. During the wintering period (mid-Oct–mid-Mar), WDLNNR converts to five main types of habitats: grassland, wet meadows, mudflats, shallow water, and open deep-waters. The hydrology of managed (R1) sub-lakes under restoration is controlled by maintaining the water-level throughout the wintering period that ensures the availability of above-mentioned heterogeneous habitats. The hydrology of un-managed (R2) sub-lakes is subject to the flooding in connected streams and "He" river, along with local rainfall [52].

2.2. Assessment of Habitat Availability

Differential hydrology has a significant impact on developing the wetland habitats of useful value for wintering migratory waterbird MSGs. To assess how fluctuations in hydrology impact habitat development or emergence at managed (R1) and unmanaged (R2) sub-lakes, Landsat satellite observation data and the GEE cloud platform were used to map land cover changes during the study period [53]. This change was then validated with daily water-depth fluctuation data by pre-deployed color calibrated PVC pipes and was finally correlated with species abundance and frequency of visits to address the suitability of managed and unmanaged habitats through selection and use.

Using GEE, an image collection was produced for a 6-month period window (Oct-March) comprising all images intersecting the study area for 2016–2017 and 2017–2018 wintering periods to produce cloud-free composite scenes with minimal snow cover. The entirety of the Sentinel 2 available for this area was also included in this analysis. After atmospheric and radiometric corrections, the resultant images were mosaic and masked with the study area and were classified into water areas, grassland, mudflat, reeds, forest land, barren land and others (settlement and cropland) using the unsupervised classification method in ArcGIS. The detailed land cover maps were validated using ground survey and aerial photos by DJI Inspire 2 [54,55].

Furthermore, we masked out agricultural land uses, poplar forest, reed plantations and settlements and focused grasslands, mudflats, deep water and shallow water types of habitats. However, due to the unavailability of high quality (e.g., free of cloud) imagery at regular intervals, we modeled the wintering habitat distribution on time series for Oct to March for the above mentioned wintering periods covering the specified dates that we had species abundance data for, using MODIS for the normalized difference vegetation index (NDVI) images at a 250 m resolution (MOD13Q1) [56,57]. We downloaded the MOD13Q1 imagery from the NASA Land Processes Distributed Active Archive Center (LPDAAC) (http://lpdaac.usgs.gov/ (accessed on 14 November 2019)). This type of information can inform habitat availability by identifying how habitat composition and structure may influence animal behaviors critical to habitat selection and use [58].

2.3. Linking Habitat Quality with Species Behavior and Network Analysis

Hydrology dependent varied availability of habitats is subject to management and conservation and has serious implications for resource availability, resource selection and use by wintering migratory waterbirds. To better understand the qualification of prevalent habitat quality for selection, we used species key behaviors (foraging and roosting) relevant to habitat selection as bioindicators of habitat quality [59,60] and assumed the quality habitat definition as "it possesses all resources (food and resting sites) needed by wintering migratory waterbirds in sufficient quantity and is being repeatedly selected for any particular use (foraging or resting) throughout wintering period".

We specifically focused on 3 basic themes by which available habitat quality, species-habitat and species-species associations can be linked: (1) direct and indirect anthropogenic factors that, in turn, impact habitat selection; (2) behavior-driven dominance of species, representing the use and consideration of behavior in structuring the community; and (3) the degree of sociality between co-occurring species, representing the use of behavior for activity persistence [44]. All three require knowledge and use of animal behavior.

2.4. Selection of Study Species

We selected five main groups of migratory waterbird species foraging during winter at WDLNNR with distinct diets [7,61] and habitat requirements (Table 1). Diet composition and availability at Dongting lake is well documented for the 14 species selected for this study [48,61–63]. While selecting species, we considered body size because large body size offers a species greater access to resources and helps to dominate over occupied habitats [64–66]. It also helps in easy and precise species identification using remote cameras. As the species were free to select any habitat and be a part of MSG, we could not control their equal representation in each group.

Table 1. Species coding, foraging guild description and habitat requirements of wintering waterbirds species covered in this study. Colored cubes identify species groups in SBAN network plots.

Spp. Code	Color Code	Description	Potential Wintering Habitat	Species
A B C D E	(orange)	Fish, clam and invertebrate eaters	Marshes and swaps along Yangzi [67] Mudflats and freshwater marshes [67] Shallow waters in lakes and streams [67] Wetlands, lakes, marshes [68,69] Marshy wetlands and rivers [67]	*Anser cygnoides* *Ardea alba* *Ardea cinerea* *Ciconia boyciana* *Ciconia nigra*
F G H	(purple)	Tuber feeder	Lakes, grasslands and marshes [67] Marshes and shallow fresh water [67] Mudflats, marshes and shallow water [67]	*Cygnus columbianus* *Grus leucogeranus* *Grus monacha*
I J K	(green)	Sedge/grass forager	Shallow fresh water and marshes [67] Lakes and marshes [67] Cropland and praires [70,71]	*Anser albifrons* *Anser fabalis* *Grus grus*
L	(blue)	Invertebrate eater	Shallow water lakes [72]	*Platalea leucorodea*
M N	(red)	Fish eater	Lakes and rivers [73] Shallow waters at freshwater lakes [67]	*Larus* spp. *Pelecanus onocrotalus*

2.5. Data Collection on Activity-Based Habitat Selection Events

We used digital video recording cameras as a sampling tool to collect ethological data on the study population of wintering migratory waterbirds MSGs [74,75] (Figure 1A). We preliminary surveyed seven sub-lakes in West Dongting Lake National Nature Reserve (under restoration and hydrological control since 2015) to allocate four sub-lakes (2 + 2 managed and unmanaged (reference) lakes) with the highest species diversity and abundance. We then installed four digital video recording cameras (DS-2DY52XZ-QG by Hik Vision, Hangzhou, China) on watch towers at a 50 m height to ensure the detection zone and perspective covering of the study sites, as well as to record habitat selection events and species behavioral abundance for resource use. We also visited each study site every second day to collect water-depth and habitat-type information (which vary by changes in the water depth) through pre-deployed color-calibrated PVC pipes that were later on used to distinguish and validate habitat types in corresponding video records. In total, we recorded over 8640 h of video footages at four study lakes and filtered best quality videos for habitat selection events between mid-October to mid-March during the 2016–2017 and 2017–2018 wintering seasons. From each selection event, we recorded behavior-based abundance data when the population density and species diversity were highest, consistent for at least an hour and distributed between pre-validated five habitat types: deep water (DW), shallow water (SW), mudflat (MF), grassland (GL) and bare ground (BG: sub-lake areas that comprise stone piles and devoid of any vegetation). For each species in a habitat, we counted their numbers foraging and roosting, while events of intra- and inter-species aggression and competition behaviors were recorded during foraging and roosting. This provided us with abundance-based data on behaviors for each species every time they selected and used a habitat.

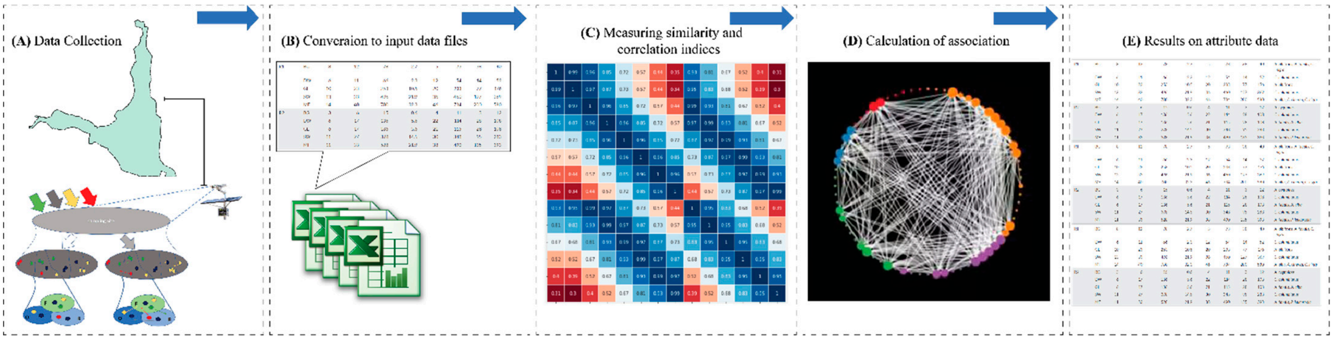

Figure 1. (**A**) Digital video recording cameras were deployed in four study lakes to collect behavior-based abundance data for each habitat they used, (**B**) data were then merged and converted to input data files, (**C**) Pearsons correlation for each study behavior was calculated for each species, (**D**) correlation values were used to plot an undirected networking diagram utilizing *i*graph and (**E**) results on network metrics and keystone species were derived. Please consult Rasool et al. [8]: Figure 5 as reference for a detailed explanation of data collection.

2.6. Social Behavioral Association Network Analysis

We applied social behavioral association network (SBAN) model to build species networks in habitats with a distinct hydrology and to calculate the degree of sociality between species (nodes). SBAN is a tetrapartite model with four parts involving: (a) habitat selection; (b) habitat overlap; (c) species-habitat associations; and (d) behavioral associations between species in shared environments. Please consult our previous study [8] for a detailed description and construction of the tetrapartite model. Based on the "conservation behavior" framework, the current study used quantitative SBAN network metrics of useful value to compare habitat quality and to answer the success extent of management treatments.

Employing the *i*graph [76] in R (R Development Core Team, 2016) for network construction, we allocated five nodes per species (i.e., five behaviors under study) and applied Eigenvector centrality to assign rankings to important species with their dominant behavior [77] accountable for community activity persistence or activity synchronization. Eigenvector centrality is extensively used in complex network theory to assess the significance of nodes in a network based on the eigenvector of the network adjacency matrix [77–79]. From an algebraic point, it is a more sophisticated view of centrality allowing for intelligentially capturing an eigenvector score that is closely related to the best rank-1 approximation for the connections to have a variable value. The PageRank algorithm used in our previous research [8] is a variant of Eigenvector centrality that could not explain the species behavioral network variation between the treatments that this study captured by utilizing Eigenvalue centrality. Using the corSparse function from Package 'qlcMatrix' [80] in R (R Development Core Team 2016), we computed Pearsons correlation and used its absolute values to draw network plots utilizing *i*graph. We estimated species' importance as the number of times a species interacted with other species and ranges between 0 and 1, where 0 indicates that species never interact, and 1 indicates maximum possible interaction in the studied network [43,81,82]. The Pearsons correlation values were used as weighted edges between the sparse matrix columns to make undirected networking plots (Figure 1). As a species in MSGs shares habitat with other co-occurring community members for any given activity, this results in interactions that may outcome in competition, consequently arise dominance (keystoneness) of some species at given habitat. Thus, within a habitat, we defined a species as important if it interacts (directly or indirectly) with other species that are in turn important. To simplify network edge density, we applied a 0.4 cutoff on correlation value and converted networking plots to the ggnetwork [83] format to highlight important connections accountable for species dominance, activity persistence and activity synchronization.

2.6.1. Aims and Assumptions

Since the study was formulated for social associations between species (degree of sociality that SBAN model explains) and species' associations with habitats, we wish to examine how well the species respond to each other and habitat quality, hence the effectiveness of management treatments.

1. We specifically hypothesized that:
2. Species are free to be or not to be part of an MSG at any time so that they can freely select or leave a pre-occupied habitat.
3. Community activity persistence solely depends upon the degree of sociality for activity synchronization within species {(*i*) or (*j*)} and between species {(*i*,*j*)}.
4. Activity synchronization in species is directly proportional to the activity (foraging and roosting) of keystone species within the community.

Species just select high quality habitats (managed or unmanaged) at random according to their need (foraging or roosting) as individual species or as MSGs with a constant probability, which is equal for both cases.

We applied this to a community of 14 species which may have up to 14 different flocks with five distinct foraging guilds (Table 1).

2.6.2. SBAN Attributes

Since we applied a networking model to calculate the interactions between the members of wintering waterbirds MSG, we specifically focused on the following attributes.

Density of the Network

We defined network edge density "d" as "the percentage of the ratio between the sum of edge weights and the number of total possible edges". Instead of the actual number of edges used in [8], we considered the sum of the actual edges weights to calculate network density.

$$\mathrm{d} = \frac{sum\ of\ actual\ edge\ weights}{number\ of\ total\ possible\ vertices} \times 100 \quad (1)$$

Degree of the Network

Interactions between nodes in a network is called the network degree [84,85]. Assume that species i and j in MSG select some habitat. Let I_t and J_t be flocks at shared time t. Species flocks meet randomly and form MSG of size n. This MSG may break up into individual species flocks in response to the behavioral coordination (aggression and/or competition with keystone species may drive a species to leave a habitat or switch to different activity). This fission and fusion of species to form or break MSG is a dynamic process that can be explained by the network degree and informs activity persistence and synchronization. We used this degree of sociality between species as the species interaction preference (SIP) and behavioral interaction preference (BIP), which can be described as:

$$SIP = log2\left(\frac{Sum\ of\ Edge's\ weights\ within\ species}{Sum\ of\ Edge's\ weights\ between\ species}\right) \tag{2}$$

and

$$BIP = log2\left(\frac{Sum\ of\ Edge's\ weights\ within\ behavior}{Sum\ of\ Edge's\ weights\ between\ behavior}\right) \tag{3}$$

where SIP can be defined as the interactions with conspecifics or between co-existing species (MSG) based on whether species *i* interacted with species *i* or *j*. The value of SIP is less than zero when the interaction is between co-existing species (*i*,*j*), while its value is greater than zero if conspecifics interact (*i*,*i*; *self-interactions*). In comparison, BIP is based on the proportion of MSG members or individual species behavior presenting how two species (*i*,*j*) responded to each other's behavior. The value of BIP is less than zero if there is inter-behavior interaction (species *i* and *j* interact with different behaviors and drive activity synchronization) within the MSG. The positive value for self-interactions in BIP (intra-behavior: different species interact with same behavior) is not accountable for activity synchronization between species.

2.7. Statistical Analysis

We acknowledge that multivariate analysis is increasingly important for investigating questions related to community ecology and dynamics [86,87]. However, these methods call for repeated measures of environmental variables that need to be standardized and correlated with species presence or absence. Having behavior-based abundance data, we therefore used Non-metric multidimensional scaling (NMDS) as the most suitable and indirect approach to produce an ordination-based distance or dissimilarity matrix [88–91]. We also applied analysis of variance test (2-way ANOVA) on studied *i*graph network attributes and antagonistic behaviors that drive sociality, remotely sensed habitat availability and habitat transition data to compare means using GraphPad Prism software (version 8.0.2).

3. Results

3.1. Habitat Selection, Species Richness and Abundance Estimates

Habitat selection by MSGs greatly differed between managed (R1) and unmanaged (R2) lakes. In managed lakes, a maximum of 56 selection events were recorded in shallow water during the study period, followed by mudflats (44), grassland (30), deep water (20) and just 3 visits in bare ground habitat. At unmanaged lakes, deep water topped with 30 selection events, followed by shallow water (27), mud flats (20), grassland (7) and four selection events at bare ground habitat (Figure 2A). Species richness also varied greatly between managed and unmanaged lakes. Comparing the number of species (*n*) in R1 and R2 lakes, mudflats at R1 lakes were the most preferred habitats that attracted all 14 species for habitat selection. Among other habitats at R1 lakes, shallow water followed by grassland, deep water and bare grounds were found to be suitable for 13, 10, six and eight species, respectively. In R2 lakes, species richness was 11 in mudflats and shallow waters, six species in both grassland and deep water, while just three species were found at bare grounds (Table 2, Figure 2B). In R1 lakes, shallow water was the most abundant habitat where 5364 birds were recorded, followed by mudflats (4945), grassland (3155), deep water (2198) and bare ground with just 370 birds. Contrarily in R2 lakes, 2684 birds were recorded in deep water, 2347 in mudflats, 2226 in shallow water, 934 in grassland habitat and just 424 at bare grounds (Figure 2C). This variation was further supported by a significant difference in all measured attributes between R1 and R2 lakes at lake (p = 0.0237) and habitat (p < 0.0001) levels (Table 3).

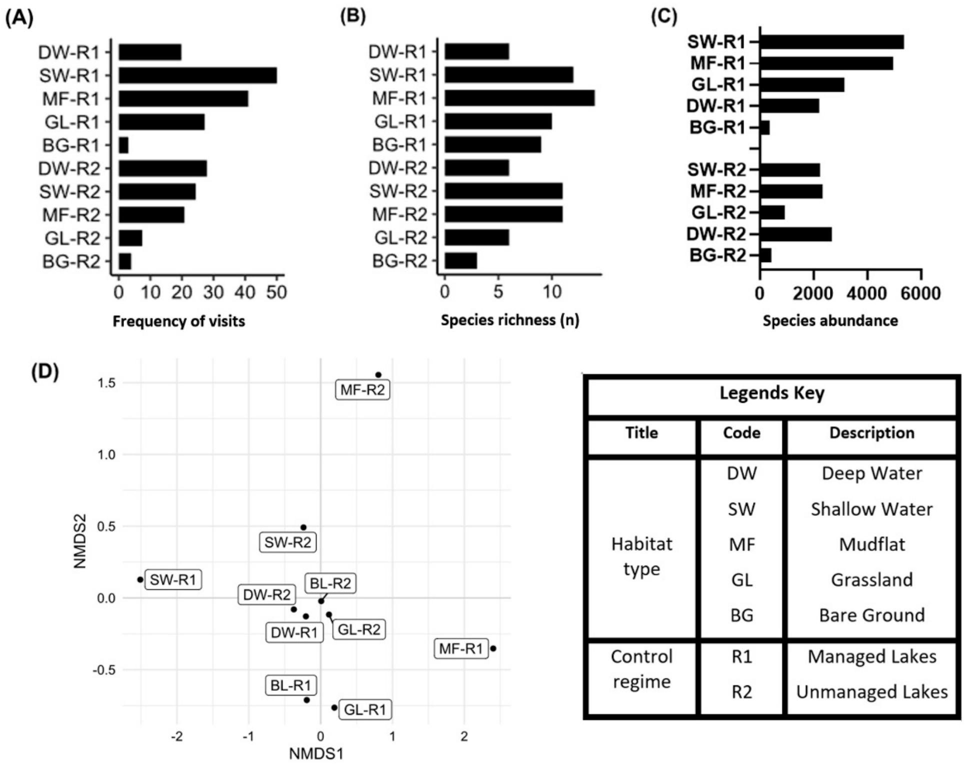

Figure 2. (**A**) Overall frequency of habitat selection by all species of MSGs at managed (R1) and unmanaged (R2) lakes, (**B**) species richness at any given habitat, (**C**) overall abundance of species (**D**) activity-based species abundance data used to calculate interactions (degree of sociality) to plot SBAN, was used to plot NMDS ordination, shows the difference in network composition and habitat use (activity) at R1 and R2 lakes.

Table 2. Social-behavioral association network metrics for activity synchrony and keystoneness at R1 and R2 lakes where "*n*" indicates species richness in each habitat.

Control Regime	Habitat	*n*	No. of Nodes	No. of Edges	Eigen Value	Edge Density	SIP	BIP	Competition	Aggression	Keystone Species
Managed lakes (R1)	Bare ground	8	12	66	2.163	0.25	−2.46	0.02	0	14	*A. albifrons*, *A. fabalis*, *C. nigra*
	Deep water	6	11	55	1.918	0.33	0.25	−2.64	55	98	*C. columbianus*
	Grass land	10	23	253	2.479	0.95	−1.05	−1.66	71	126	*A. albifrons*
	Shallow water	13	33	528	4.498	2.6	−1.89	−1.58	53	238	*C. columbianus*
	Mud flat	14	40	780	3.834	2.9	−1.94	−1.39	98	176	*A. alba*, *A. cinerea*, *C. nigra*
Unmanaged lakes (R2)	Bare ground	3	6	15	0.700	0.06	1.36	−3.51	0	12	*A. cygnoides*
	Deep water	6	17	136	2.495	0.73	−1.22	−2.08	119	177	*C. columbianus*
	Grass land	6	17	136	1.969	0.6	−0.39	−2.41	8	52	*A. fabalis*, *A. alba*
	Shallow water	11	27	351	2.234	1.18	−2.15	−1.55	82	128	*C. columbianus*
	Mud flat	11	33	528	3.431	2.05	−1.89	−1.77	107	78	*A. fabalis*, *P. leucorodea*

Table 3. A 2-way analysis of variance test was employed to compare means of constructed SBAN networks and to check significant difference at the treatment level (R1 and R2) and habitat level within treatments, NDVI based habitat areas between treatments and within treatments as well as habitat transitions in both treatments for habitat availability.

Source of Variation	DF	Sum of Squares	Mean Square	p Value	Significance Level
Interaction [1]	11	25,753	2341.2	$p = 0.0249$	*
Network metrics [1]	11	759,260	69,024	$p < 0.0001$	****
Lakes [1]	1	5530.9	5530.9	$p = 0.0237$	*
Habitats [1]	48	575,435	11,988	$p < 0.0001$	****
Interaction [2]	7	13.58	1.939	$p = 0.0001$	***
Habitat areas between treatments [2]	7	59.74	8.534	$p < 0.0001$	****
Wintering periods [2]	1	0.6547	0.6547	$p = 0.0285$	*
Habitat Areas among wintering periods [2]	8	0.3665	0.04581	$p = 0.8281$	Not significant
Habitat transition between treatments [3]	16	33.65	2.103	$p = 0.0113$	*

[1] We employed 2-way ANOVA to check the significant difference between network attributes at the lake and habitat level, [2] between habitat area at the treatment level and study duration and [3] habitat transitions at treatment level over the study duration. * significant; *** very significant, **** highly significant.

3.2. Species Keystoneness and Activity Synchrony Through Species Interaction Preference (SIP) and Behavior Interaction Preference (BIP)

In managed lakes, *Anser albifrons* was the keystone at grassland and three species (*Area alba*, *Ardea cinerea and Ciconia nigra*) were keystones at mudflat habitats. *Anser albifrons*, *Anser fabalis* and *Ciconia nigra* were keystones at bare-ground type of habitats. Contrarily at unmanaged lakes, *Anser fabalis* and *Ardea alba* were keystones at grasslands, while *Anser fabalis* and *Platalea leucorodea* were keystones in mudflat habitat while *Anser cygnoides* was the keystone at bare grounds. However, *Cygnus columbianus* appeared as keystone species in deep water and shallow water habitats at both R1 and R2 lakes. These findings were further supported by NMDS ordination where besides deep-water habitats, other habitats were far dissimilar in terms of species network composition and degree of sociality at both managed and unmanaged lakes (Table 2, Figure 2D).

Besides deep water (0.25) habitats at managed lakes, species interacted with other species and maximum interaction scores (SIP) were found in bare grounds (−2.46) followed by mudflats, shallow waters and grassland habitats with −1.94, −1.89 and −1.05 scores, respectively. At unmanaged lakes, shallow waters (−2.15) followed by mudflats, deep water and grassland showed inter-species (SIP) interactions with −1.89, −1.22 and −0.39 scores, respectively. Among both control regimes, bare ground (1.36) in unmanaged lakes had maximum intra-species SIP interactions (Table 2). The BIP score at deep water habitat was −2.64, which was the maximum among all habitats in managed lakes, followed by grassland (1.66), shallow water (−1.58) and mudflat (−1.39). At unmanaged lakes, BIP ranged a maximum of −3.51 in bare ground habitat, followed by grassland, deep water mudflat and shallow water (−2.41, −2.08, −1.77 and −1.55), respectively (Table 2).

3.3. Habitat Structure over Time

The normalized difference vegetation index was used to calculate the habitat area for deep water, shallow water, mudflat and grassland for two wintering periods (Figure 3a,b). At managed lakes (R1), the grassland habitat area was increased by 46.69%, deep water was increased by 20.88%, while shallow water and mudflat habitat areas were decreased by 54.31% and 19.54%, respectively, over the study period. At unmanaged lakes (R2), mudflat, grassland and deep-water areas were increased by 53.89%, 20.20% and 8.26%, respectively, while shallow water area was decreased by 57.72% (Figure 3d). Using a 2-way analysis of variance (ANOVA) test, we found a significant difference ($p < 0.0001$) in habitat areas at both treatment levels but no difference was found among two wintering seasons (2016–2017 and 2017–2018) in both treatments. We then checked transition in habitat areas between one habitat to another and found that habitat conversion significantly differed (p = 0.0113) between the treatments during the study period (Table 3, Figure 3c).

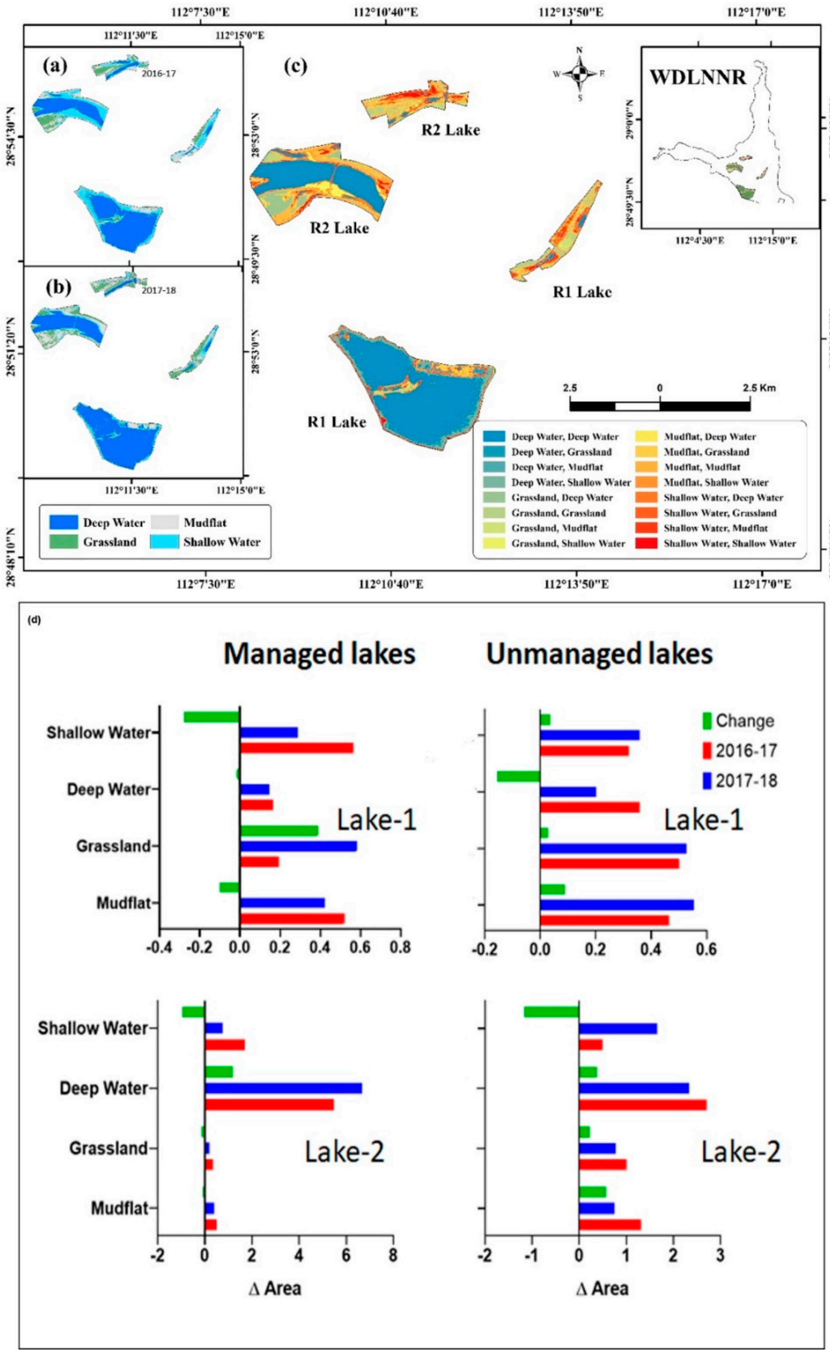

Figure 3. Habitat areas calculated from classified NDVI maps developed for 2016–2017 (**a**) and 2017–2018 (**b**) wintering periods were analyzed to detect change or conversion of one habitat type to another in each study lake (**c**). (**d**) change in habitat areas plotted for each study lake during study duration.

4. Discussion

4.1. Habitat Quality Alters Species Behavior and Network Structure

One way to compare habitat quality is to observe species behavioral response under the null hypothesis of species independence to select a habitat [61,92,93]. In unmanaged lakes, our findings demonstrate that species richness, species abundance and frequency of habitat selection remained lower than that of at managed lakes. Besides *Anser fabalis*, *Ciconia boyciana* and *Ciconia nigra*, all other species were abundant in managed sub-lakes, indicating better quality habitats at R1. In community ecology, good habitat conditions invite certain species to share the resources and reduce community composition when conditions decline [34]. In this situation, information is shared by the activities of a species, so that knowing the location of one species location with activity at a particular point in a shared environment provides strong insights into the contemporary presence of other species and their activities at same location. For instance, this claim was supported by our finding of *Cygnus columbianus*, which was found to be dominant in deep water and shallow water habitats of both managed and unmanaged lakes, shared shallow habitats with almost same species in both R1 and R2 lakes (Table 2). Species that take seasonal population-migrations are likely to exhibit this kind of information sharing [27,43,94].

We also witnessed higher species richness and abundance at managed lakes that pointed to better quality habitats and their continuous availability throughout wintering season than at unmanaged lakes (Figure 2B,C). The MSGs structure for wintering waterbirds extensively relied upon social interactions between species. Mammides et al. [28] described differences in MSGs structure and composition for a function of social interactions and habitat quality that generate nonrandom organizations of flocks and communities in varying environments. Meanwhile, keystone or more dominant species play a pivotal role in structuring community, habitat selection and exploitation. The frequent habitat selection by a particular species or MSG increases the probability of habitat suitability [71], particularly for foraging and roosting, which in our case was seen in mudflat and shallow water habitats at managed lakes (Figure 2A).

Martin et al. [95] said habitat selection by animals at shared spatial and temporal scales reveals suitability features more important to fitness than selection made at finer scales. The shared spatial scale (heterogeneous habitat) examined in this study showed the same robust pattern, suggesting that habitat heterogeneity, their continued availability, and management are important predictors of habitat selection for migratory waterbirds MSGs at wintering grounds. Zhu et al. [7] and Bennet et al. [96] demonstrated resource selection in species as an important component of habitat ecology while animal behavior in a particular environment reflects the state of available resource quality and availability. As we hypothesized, results on frequency of habitat selection indicate that behaviors centered at habitat selection (foraging and roosting) have revelation with available habitat quality. At managed sub-lakes, species abundance and repeated mudflat habitat selection and use by 14 species indicated its high quality, suitability and continuous availability of resources (food and shelter) throughout the wintering period (Figure 2A,B; Table 2).

4.2. Social Interactions Alter Network Structure

Species behavioral interaction networks offer insights on habitat quality and community dynamics in differentially managed ecosystems. Social interactions shape the structure of MSGs and relationships between species adjust the response to available habitat for exploitation in shared environments [8,93]. Confirming these relationships, we identified body size as a factor that explains interaction patterns for dominance, both between the closely related species and phylogeny. Large body size of *Cygnus columbianus* helped the species to dominate over deep water and shallow water habitats and to control the activities of peripheral c-existing species in both lake types (Figure 4). This overall mass-to-dominance relationship has been previously demonstrated in birds and animals [3,66,97,98]. It is prevalent through literature that intransitivity in dominance relationships promotes species coexistence [3,99]. In mudflats and shallow water habitats of managed lakes, we found few well-supported intransitive relationships between plausible spatial competitors at the 3-, 4- and 5-species subnetwork clusters. Specifically, we found the *Grus leucogeranus*, *Grus monacha*, *Ciconia nigra* and *Anser albifrons* subnetwork to be intransitive in managed lakes and shallow water habitats. *Ciconia nigra* was dominant to *Grus monacha* and *Anser* *albifrons*, while *Grus leucogeranus* was dominant to *Anser albifrons*. This dominancy was a function pattern of social interactions, especially aggression, that made subordinate species synchronize activities (foraging and roosting) with dominant species (Figure 4).

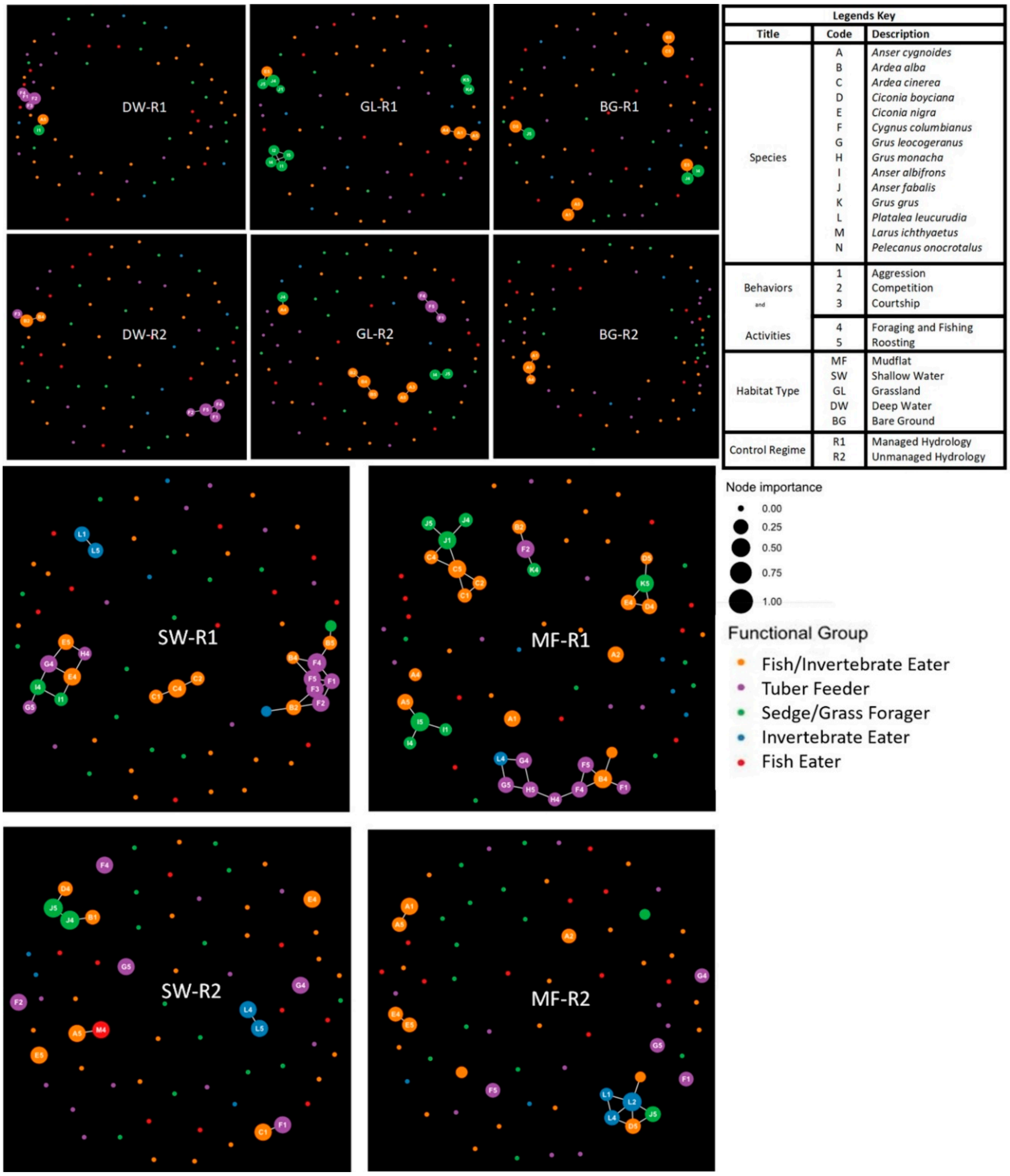

Figure 4. Undirected network graphs plotted using *i*graph were converted to ggnetwork format for independent assessment of all 5 habitat types in both managed and unmanaged lakes to relate keystone species personality for control or dominance over peripheral co-existing species. Regime-wise comparison was carried out for network composition based on Pearson's centrality measures with an arbitrary cutoff of 0.4 to highlight activity-based important nodes and their connections.

Another intransitive subnetwork of 5-species comprised of *Ardea alba*, *Cygnus columbianus*, *Grus leucogeranus*, *Grus monacha* and *Platalea leucorodea* was seen in mudflats at R1. Here, *Cygnus* spp. dominated over *Ardea alba*, while *Grus monacha* behaved like a central hub which along with *Platalea* spp. were dominated by *Grus leucogeranus*. In the same way as for a shallow water habitat, the dominance here was also a function of animal personality (sociality) for foraging and roosting activities mutually synchronized between these species to avoid competition. This activity regulatory paradigm (synchronization) is a state where changes are initiated within small networks (within and between species or within and between behaviors) due to community activity. These regulatory mechanisms are prevalent throughout nature, occurring in vastly different systems and levels of organization [28,100,101].

4.3. Hydrology as Key Element for Structuring and Development of Wintering Habitats

Our results indicate effects of hydrology, even uncontrolled, considerably contribute to habitat availability and ultimately impact selection. Managing hydrology is especially effective for maintaining wintering waterbirds' whole metapopulation through maintaining a heterogeneous habitat [34,102]. Based on our results, controlled water levels improved the effectiveness of management and conservation efforts. In mosaic landscapes like WDLNNR, controlling and management of water-levels could successfully offer a desired habitat distribution suitable for wintering waterbirds (Figure 3). Land use practices are likely the most important human-mediated processes influencing habitat selection by waterbirds [93,103]. Therefore, we sought to understand how the current composition and distribution of habitats were impacting the selection, use and temporal availability of wintering grounds. Our findings revealed that water depth is an important driver in shaping habitat availability and distribution in the managed as well as at unmanaged lakes, as stated by [40,48,49,63,93,104–106]. We found that uncontrolled events of flooding had the strongest negative effect on mudflat and shallow water habitat availability and selection. Preceded by the effects of controlling water depth, habitat diversity at managed lakes attracted more species diversity and abundance, but overriding numbers resulted in more competition and aggression events (Figure 2C, Table 2). It was surprising to find that *Ciconia nigra* numbers at unmanaged lakes (142) was higher than that of at managed lakes (121) (see Appendix A for habitat wise species abundance data for R1 and R2). This might be a reason how lower species diversity and abundance may pose less competition to the co-existing species and offer increased availability of food in natural streams.

Although broad-scale processes like land use or climate gradients almost certainly influence distributions of many species, the ability to detect their effects is often limited by sampling constraints [17,106]. Behavior based abundance data at each lake offered relatively fine scale samples, leading to increasingly reliable results for wintering waterbirds' preferred habitats. Closer examination of social behavioral association network clusters suggested that activities of waterbirds on managed lakes were fairly consistent across available habitat types (Figure 4), with foraging and roosting accounting for the highest proportions of behaviors. Except for reduced species richness and frequency of selection of bare grounds, all habitat types supported the finding that wintering waterbirds use properly managed habitats that assure adequate resources (food and shelter) throughout the wintering period. Resources within each habitat type, however, are likely to fulfill different dietary requirements [7,47,93]; we identified heterogeneous habitats of suitable selection value that order selection by wintering waterbirds' MSGs.

5. Conclusions

Management's impact on wintering habitat quality and use by wintering migratory waterbirds was studied by utilizing social behavioral association network approach. The complex behavioral networks of species in differentially managed lakes differed in structure, composition and species-habitat associations. Utilizing behavior as a bioindicator of ecosystem health, we examined how experimental restoration treatments (hydrological control) influenced habitat selection, species behavior and habitat use and evaluated the success of restoration/management treatments. This study provided a unique opportunity to understand the connections between restoration ecology, behavioral ecology and habitat ecology using a conservation behavior framework. Integrating information as well as insights gained in this study can help make management more effective, efficient and responsive to environmental changes.

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Informed Consent Statement: Not applicable.

Data Availability Statement: The data used to construct SBAN can be accessed on google drive via the link provided: https://drive.google.com/file/d/1kF7EnUnVM0uc8A-xQYe2C165exu1Vfsm, accessed on: 4 February 2021.

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Conflicts of Interest: We do not have any conflict of interest to declare.

Appendix A

Table A1. Species abundance and distribution in habitats at managed lakes (R1).

Species	Shallow Water	Deep Water	Mud Flat	Grass Land	Barren Land	Total
Anser albifrons	340	88	305	1569	127	2429
Anser cygnoides	43	39	190	515	74	861
Anser fabalis	16	N/A	207	414	5	642
Ardea alba	583	24	305	128	19	1059
Ardea cinerea	766	71	798	37	17	1689
Ciconia boyciana	1	N/A	19	N/A	N/A	20
Ciconia nigra	25	N/A	88	2	6	121
Cygnus columbianus	2348	2045	1180	403	96	6072
Grus grus	3	N/A	5	42	N/A	50
Grus leucogeranus	20	N/A	114	12	N/A	146
Grus monacha	6	N/A	72	3	N/A	81
Larus ichthyaetus ichthyaetus	26	9	16	N/A	2	53
Pelecanus onocrotalus	N/A	N/A	5	N/A	N/A	5
Platalea leucorodia	1580	N/A	1409	N/A	N/A	2989

Table A2. Species abundance and distribution in habitats at Unmanaged lakes (R2).

Species	Shallow Water	Deep Water	Mud Flat	Grass Land	Barren Land	Total
Anser albifrons	323	277	166	49	N/A	815
Anser cygnoides	30	N/A	120	198	75	423
Anser fabalis	24	N/A	83	138	N/A	245
Ardea alba	206	151	208	46	N/A	611
Ardea cinerea	342	101	426	5	N/A	874
Ciconia boyciana	4	N/A	6	N/A	N/A	10
Ciconia nigra	38	N/A	104	N/A	N/A	142
Cygnus columbianus	1366	2395	648	342	333	5084
Grus leucogeranus	9	N/A	60	N/A	N/A	69
Larus ichthyaetus ichthyaetus	10	1	14	N/A	N/A	25
Platalea leucorodia	207	2	345	N/A	N/A	554

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