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Spatial patterns of breeding colonies of Great Cormorant (*Phalacrocorax carbo*) and Palas's Gull (*Larus ichthyaetus*) on Kitay Island in the Central Sivash lagoon system

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Abstract

This study analyzes the spatial distribution patterns of breeding colonies of Great Cormorants (*Phalacrocorax carbo*) and Palas's Gull (*Larus ichthyaetus*) on Kitay Island in the Central Sivash lagoon system. Using spatial point pattern analyses, we quantified clustering and dispersion at multiple spatial scales. Our results reveal a marked contrast in nesting strategies: Great Cormorant nests exhibited strong, statistically significant clustering (mean Nearest Neighbor Distance, NND = 0.23 m; Moran's I = 0.34, p = 0.02) and significant positive spatial autocorrelation, consistent with colonial breeding. In contrast, Palas's Gull nests were significantly more dispersed (mean NND = 0.67 m) and showed no significant spatial autocorrelation, reflecting territorial nesting behavior. Cross-species analysis indicated moderate spatial segregation, evidenced by a negative correlation of nest densities (r = -0.56) and Ripley's cross K-function, suggesting niche partitioning that facilitates coexistence. These findings quantitatively highlight distinct nesting ecologies and emphasize the critical importance of integrating spatial ecology into conservation planning for colonial waterbirds in saline lagoon islands. The study provides new quantitative baselines crucial for effective monitoring and habitat management in the Azov-Black Sea region.

Keywords
Great Cormorant, Palas's Gull, spatial point pattern, Ripley's K function, nest clustering, colonial waterbirds, Kitay Island, Sivash lagoon, avian spatial ecology, conservation planning

Introduction

Breeding colonies of colonial waterbirds exhibit complex spatial architectures that arise from a confluence of ecological pressures, behavioral adaptations, and environmental constraints. These distribution patterns, ranging from dense clusters to dispersed territories, are not random but are strategic responses to factors such as predator avoidance, resource competition, and social dynamics. For instance, in ground-nesting Great Cormorants (*Phalacrocorax carbo* Linnaeus 1758), the presence of predators like the Red Fox (*Vulpes vulpes*) has been shown to drive a proactive adjustment in colony structure, leading to significantly higher nest densities, shorter Nearest Neighbor Distances (NNDs), and a shift towards a contagious, clustered distribution, ultimately resulting in a more circular colony shape to reduce the edge-to-surface ratio and mitigate predation risk [van Eerden & van Eerden 2022). A comprehensive understanding of this spatial organization is therefore fundamental to avian ecology, offering insights into population dynamics, species interactions, and habitat requirements that are critical for effective conservation management.

The island complexes of the Central Sivash, a vast saline lagoon system in the Azov-Black Sea region, provide indispensable breeding habitats for numerous colonial waterbird species. Kitay Island, in particular, serves as a key breeding site for significant populations of the Great Cormorant and the Great Black-headed Gull or Pallas's Gull (*Larus ichthyaetus*, Pallas, 1773). The Pallas's Gull is a large, fish-eating predator listed as a recovering species in the Red Book of the Russian Federation (Golubev 2023a), and its populations are demonstrating significant northward expansion, using reservoirs as key distribution corridors (Golubev 2023b). This species has shown a remarkable capacity for rapid population growth in new habitats, as evidenced by the colony on the Novosibirsk Reservoir (Siberia), which grew from a single pair in 1994 to 900-1400 nests by 2015 (Andreenkov et al. 2015). Colonies of this species can be highly dynamic; for example, on Lake Aike in the Orenburg region, the number of breeding pairs fluctuated dramatically from 270 nests in 1998 to zero in dry years, rebounding to 207 in 2004 (Barbazyuk 2020). Furthermore, Pallas's Gulls exhibit high adaptability in their nesting strategies, forming dense colonies or spatially separated subcolonies, often alongside other larid species (Barbazyuk 2020). However, their reproductive success is heavily influenced by a complex interplay of ecological and social factors, including predation by other gulls like the Steppe Gull (*Larus* (*cachinnans*) *barabensis*), which can destroy up to 53% of eggs and young chicks, and a surprising lack of effective anti-predator behavior despite their large size (Panov & Zykova 1987). As prominent piscivores, these species function as vital indicators of the ecological health of the Sivash wetlands. Despite their importance, a quantitative understanding of their fine-scale spatial ecology on Kitay Island remains limited, with existing studies often focusing on broader population surveys rather than the structural configuration of their colonies (Siokhin & Matsyura 2025).

Studying the distribution of colonial birds on small islands is crucial for understanding their breeding ecology and population dynamics. These islands often serve as key nesting sites, offering unique habitats that influence colony size and structure. Monitoring distribution patterns helps detect environmental changes and human impacts, guiding effective conservation strategies. Moreover, such studies provide insights into island ecosystem health and biodiversity maintenance, which are vital for preserving delicate island environments.

Previous research in other systems has effectively utilized spatial analysis to unravel interspecific relationships. Studies have documented the spatial interplay between cormorants and gulls, often highlighting competitive interactions (Matsyura 2000; Somers et al. 2007, 2011), while others have explored the foraging ecology and niche partitioning of Palas's Gull (*Larus ichthyaetus*, Pallas, 1773) and Double-crested Cormorants (*Nannopterum auritum* Lesson, 1831) (Lyons et al. 2009; Seefelt & Farrell 2018). However, a notable research gap exists concerning the specific spatial relationship between the Great Cormorant and the Pallas's Gull, two dominant and ecologically influential species within the Sivash avifauna. The mechanisms that allow for their coexistence, whether through spatial segregation, habitat partitioning, or tolerance, are not yet understood. This is particularly relevant given that Pallas's Gulls are known to form mixed colonies with other larid species (Andreenkov et al. 2015; Barbazyuk 2020) and their expansion into new areas could intensify competition for nesting space. Moreover, understanding colony formation is critical, as species like the Pallas's Gull are considered "nomadic" and form colonies via an "accelerated type," where social bonds are strong but attachment to a specific territory is weak, allowing them to exploit temporary "ecological windows" in unstable environments (Kharitonov 1999; Barbazyuk 2020).

To address this gap, our study employs a suite of spatial point pattern analyses, including nearest neighbor distance (NND) calculations and Ripley's K-function. These powerful methods allow for the quantitative characterization of nest distribution patterns, moving beyond descriptive accounts to statistically test for clustering, dispersion, or randomness across multiple spatial scales. Furthermore, these tools can elucidate interspecific relationships by revealing significant spatial segregation or aggregation between species. Our study aims to: 1) quantify the intra-specific nesting patterns of Great Cormorants and Pallas's Gull on Kitay Island, and 2) determine the nature of their inter-specific spatial relationship.

Materials and methods

Study site and field data

The study was conducted during the 2021 breeding season on Kitay Island, Central Sivash lagoon (coordinates 46°03′44″ N, 34°20′23″ E, top elevation point is about 3.5 m above water surface). This is the mainland-origin island, characterized by dominant meadow-steppe vegetation (genera *Bromus*, *Elytrigia*, and *Atriplex*), with projective cover reaching 100% in its central part (Fig. 1). Ongoing coastal erosion has led to a reduction in the island's area (from 3 hectares in the 1980s to 2 hectares at present). Our significant long-term data for this site begin with the first recorded presence of the Pallas's Gull in 1949, followed by the colonization of the island by the Great Cormorant in 1990. Due to the vulnerability of the bird community, we restricted our research during multiple site visits and did not conduct studies on nest distribution patterns to minimize disturbance. In 2021, the direct nest counts and individual bird counts were conducted at seven Great Cormorant colonies and two Palas's Gull colonies using UAVs, supplemented by binocular observations and photographic documentation (Figs 2, 3).

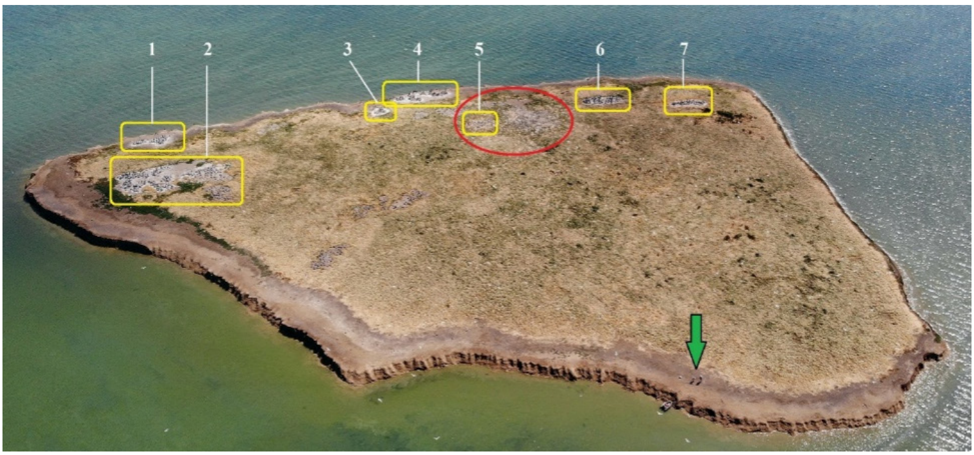

Figure 1. Kitay Island with Great Cormorant (1–7) and Palas's Gull (red circle) colonies distribution. Green arrow indicates the observation point.

Aerial image acquisition

High-resolution aerial imagery was acquired using a DJI Mavic 2 Pro Unmanned Aerial Vehicle (UAV) equipped with a 20-megapixel RGB sensor. All surveys were conducted during the peak incubation period to maximize nest occupancy and visibility. Flight missions were programmed and executed autonomously using DJI Pilot 2 software to ensure systematic coverage of the entire colony area. Flights were performed at an altitude of 80-100 meters above ground level, yielding a ground sampling distance (GSD) of 2.0–2.5 cm/pixel. To minimize disturbance to the breeding birds, operations were restricted to periods of favorable weather (wind speed < 8 m/s, no precipitation). A consistent flight plan with 80% frontlap and 70% sidelap was used to ensure sufficient image overlap for photogrammetric processing.

Photogrammetric processing and map generation

The collected aerial images were processed using Agisoft Metashape (Version 1.8.5) photogrammetric software to generate a seamless, georeferenced environmental model. The processing workflow included: (1) alignment of images and generation of a sparse point cloud; (2) building a dense point cloud; and (3) construction of a high-resolution digital surface model (DSM) and an orthorectified mosaic (orthomosaic). Spatial accuracy was validated using ground control points (GCPs) surveyed with a Real-Time Kinematic (RTK) GPS receiver, resulting in a final orthomosaic with a root-mean-square error (RMSE) of less than 5 cm.

Figure 2. Great Cormorant nest locality.

Nest delineation and validation

Active nests were identified and manually digitized as point features from the orthomosaic using ArcGIS Pro (Version 3.1). A nest was classified as active based on the clear presence of an incubating adult or eggs. The point was placed at the estimated center of the nest cup. To ensure mapping accuracy, this process was conducted independently by multiple trained observers. A subset of nests (X%) was cross-validated against ground-truthed observations collected from discreet vantage points using binoculars and telephoto lenses to confirm classification accuracy.

Figure 3. Palas's Gull nest locality.

Spatial point pattern analysis

The georeferenced point layer of nest locations was used for all subsequent spatial analyses. We employed a suite of spatial statistics to quantify the distribution patterns of nests for each species:

- Nearest Neighbor Distance (NND): The mean Euclidean distance from each nest to its closest conspecific neighbor was calculated using the 'Generate Near Table' tool in ArcGIS. The mean NND and standard deviation were computed to quantify baseline nest spacing.
- Ripley's K-function: To analyze spatial clustering or dispersion across a range of spatial scales, we computed Ripley's K-function using the 'spatstat' package in R (Dixon 2002). The observed K-function was compared to a theoretical distribution of Complete Spatial Randomness (CSR) using Monte Carlo simulation envelopes (n = 999) to determine significant departures at specific distances.
- Spatial Autocorrelation: Global spatial autocorrelation was assessed using Moran's I index to determine if nest locations exhibited a statistically significant

clustered, dispersed, or random pattern across the entire colony (Skórka et al. 2016). Interspecific spatial relationships were examined by testing for a correlation between the densities of Great Cormorant and Palas's Gull nests across the study area and by analyzing bivariate point patterns.

Statistical Analysis

All statistical analyses were performed in R (Version 4.4.3). Descriptive statistics, including means, standard deviations, and coefficients of variation (CV), were calculated for nest counts and spacing metrics. An independent samples t-test was used to compare the mean NND between the two species. The Kolmogorov-Smirnov test was applied to compare the overall distribution functions of the NNDs for both species. Pearson's correlation coefficient was used to assess the relationship between the spatial densities of the two species' nests. For all tests, the significance level was set at $p = 0.05$.

Results

Spatial distribution of nesting colonies

Mapping of nest locations revealed distinct spatial patterns in colony organization on Kitay Island. Great Cormorant nests (Fig. 4) were clustered strongly in specific localized areas, with nests often spaced closely together, indicative of colonial breeding behavior. Palas's Gull nests (Fig. 5), in contrast, showed a more dispersed distribution with wider spacing between nests (Table 1).

The mean nearest neighbor distance for Great Cormorants was 0.23 meters (SD = 0.15 m), reflecting tight clustering within colonies. Palas's Gull had a significantly higher mean NND of 0.67 meters (SD = 0.22 m; t-test, $p < 0.001$), consistent with more evenly spaced nesting sites.

Table 1. Spatial point pattern analysis results for Great Cormorant and Palas's Gull nesting colonies on Kitay Island

Metric	Great Cormorant	Palas's Gull
Number of Nests	483	185
Mean Nearest Neighbor Distance, Mean±SD (m)	0.23 (± 0.15)	0.67 (± 0.22)
Moran's I (Spatial Autocorrelation)	0.34 ($p = 0.02$)	0.07 ($p = 0.40$)
Ripley's K Function Interpretation	Significant clustering ($p < 0.01$)	Random to slightly regular spacing

Figure 4. Great Cormorant nests.

Figure 5. Palas's Gull nests.

Ripley's K function analysis

Ripley's K function was used to quantitatively assess spatial clustering at multiple scales (Delfino 2023). For Great Cormorants, the empirical K function lay significantly above the expected value under Complete Spatial Randomness (CSR) for distances up to approximately 30 meters, strongly indicating clustering at scales relevant to nest spacing and colony size. This pattern is the direct multi-scale expression of the extremely dense packing of nests, quantified by the mean nearest neighbor distance of just 0.23 m. Monte Carlo simulation envelopes confirmed statistical significance ($p < 0.01$).

For Palas's Gull, the Ripley's K curve hovered near or below CSR expectations at most scales, indicative of random to regular dispersion. This result aligns with the species' territorial behavior, which enforces a much larger average inter-nest spacing (mean NND = 0.67 m), preventing the formation of dense clusters and leading to a more uniform or random distribution across the colony.

Spatial Autocorrelation

Moran's I spatial autocorrelation coefficient was significantly positive for Great Cormorant nests ($I = 0.34$, $p = 0.02$), indicating strong spatial dependence among neighboring nests and reinforcing the finding of an intensely clustered colony structure, as evidenced by the very low mean nearest neighbor distance of 0.23 m. Conversely, Palas's Gull nests showed no significant spatial autocorrelation ($I = 0.07$, $p = 0.40$), corroborating observations of spatially independent nest placement and their significantly larger mean spacing of 0.67 m.

Inter-species Spatial Relationships

Cross-species spatial statistics revealed moderate spatial segregation between Great Cormorant and Palas's Gull, reflected in a significant negative correlation of nest densities ($r = -0.56$, $p < 0.05$). Ripley's cross K-function further indicated avoidance or niche partitioning, likely driven by interspecific competition or differing habitat preferences (Fig. 6). This segregation is physically manifested in the stark contrast between the cormorants' densely packed clusters (mean NND = 0.23 m) and the gulls' dispersed territories (mean NND = 0.67 m).

The overall spatial distribution of nests across the study site was found to be non-random (Quadrat test, $\chi^2 = 18.52$, $df = 9$, $p = 0.03$), indicating that nest placement is influenced by factors other than chance. The highly specific nest spacing of each species, namely the extreme clustering versus loose dispersion, is a primary driver of this non-random, segregated pattern at the landscape level. These spatial segregation patterns suggest niche differentiation that reduces direct competition for nesting space and facilitates coexistence of the two species within the limited island habitat.

The Cormorant curve lying significantly above the envelope indicates clustering, while the Palas's Gull remaining within or below the envelope indicates a random to regular distribution.

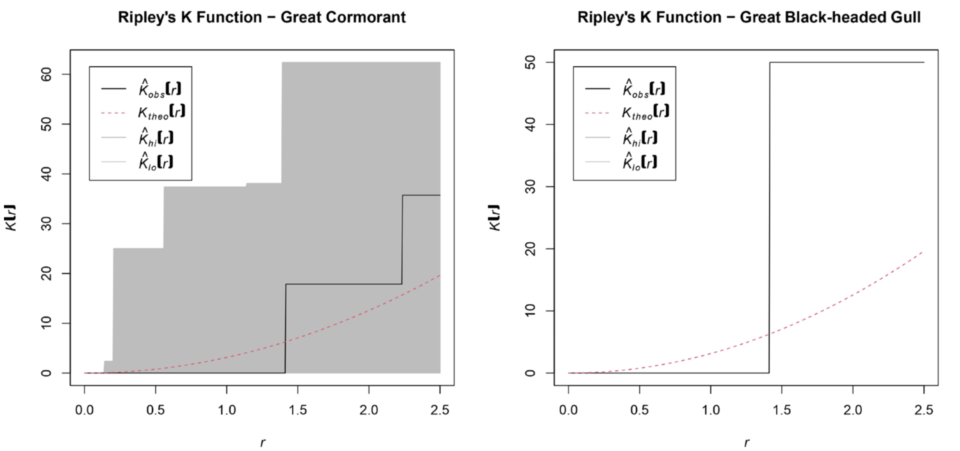

Figure 6. Ripley's L-function plots for Great Cormorant and Palas's Gull nests. The L-function, a transformation of Ripley's K, is plotted against distance (r). The solid blue line represents the observed L(r) for Great Cormorants, and the solid red line for Palas's Gulls. The dashed black line (theoretical L(r) = r) represents the expected value under Complete Spatial Randomness (CSR). The grey bands represent the simulation envelopes under CSR.

Discussion

Our study provides a quantitative analysis of the spatial nesting ecology of Great Cormorants and Palas's Gull on Kitay Island, revealing a system of strong interspecific segregation driven by contrasting breeding strategies. The results demonstrate that the colonial, clustered nesting of Great Cormorants and the dispersed, territorial nesting of Palas's Gull are not merely behavioral observations but are statistically distinct spatial patterns with clear ecological consequences. Critically, the observed niche partitioning, evidenced by a negative correlation in nest densities and cross-species spatial analysis, likely reduces direct competition for nesting space, facilitating coexistence within the limited insular habitat.

The strongly clustered configuration of Great Cormorant nests, confirmed by multiple spatial statistics (NND, Ripley's K, and Moran's I), is consistent with their well-documented colonial breeding behavior. This clustering can be interpreted through the lens of the "ecology of fear." As demonstrated by van Eerden & van Eerden (2022) for ground-nesting Great Cormorants, increased predator presence directly drives a pro-active adjustment in colony structure, leading to higher nest densities and shorter Nearest Neighbor Distances (NNDs). The authors found that nests shifted from a dispersed or random pattern to a significantly clustered, contagious distribution in response to predators like the Red Fox, a strategy aimed at reducing the edge-to-surface ratio and mitigating predation risk, even though breeding at the fringe still incurred greater losses. Furthermore, this high-density clustering carries intrinsic costs, including increased intraspecific aggression, interference leading to reduced breeding success, and adults being soiled by excrement from neighbours (van Eerden & van Eerden 2022). For the Great Black-headed Gull, the significantly larger NND values confirm a dispersed pattern; however, it is noteworthy that this spacing did not occur at the expense of reproductive success within the observed range.

This fundamental difference in breeding strategy creates the underlying template for the spatial organization observed on Kitay Island. Our findings of spatial segregation are also consistent with studies of other sympatric waterbirds. For instance, in a mixed breeding site in Korea, Great Cormorants were observed to occupy the central breeding grounds previously used by Ardeidae species in the following year, while the herons and egrets moved to nest around the cormorant colony, indicating interspecific interactions in space usage (Lee et al. 2019). This suggests cormorants may either move to favourable nest sites or select sites used by other species in the previous year. The intense clustering of Great Cormorants on Kitay Island may thus represent a pro-active anti-predator strategy, as described by van Eerden & van Eerden (2022), even in the absence of observed predation during our study. The authors noted that such structural adaptations are often made early in the season, based on previous years' experiences, and can persist even if predator pressure fluctuates.

The segregation we observed suggests that the two species may also be selecting nesting sites based on microhabitat preferences or in response to the presence of the other, thereby avoiding the potential negative impacts of close co-nesting. This is particularly relevant for the Great Black-headed Gull, which exhibits a "primitive" colonial structure with a surprising lack of nest-site fidelity from year to year and a random choice of nest location within the colony area (Kharitonov 2021). This low intraspecific cohesion and absence of a defined colony macrostructure could make them particularly vulnerable to displacement by a densely packed and expanding species like the Great Cormorant. Furthermore, the Great Black-headed Gull shows a complete lack of anti-predator behaviour towards other bird species, allowing predators like the Yellow-legged Gull (*Larus cachinnans*) to steal eggs and chicks with impunity (Panov & Zykova 1987; Mierauskas & Buzun 1991). This documented vulnerability to interspecific aggression and predation likely reinforces the need for spatial separation from other colonial species, including cormorants whose dense colonies could attract such predators and kleptoparasites.

The implications of this spatial structure are critical for conservation. The study by Seefelt and Farrell (2018) serves as a stark warning, demonstrating that management actions targeted at one species (Double-crested Cormorants) can have severe indirect negative consequences on a co-nesting species (Palas's Gull), including increased disturbance and reproductive failure. Furthermore, the work of van Eerden & van Eerden (2022) highlights that high-density clustering, while an anti-predator strategy, carries its own costs, including increased intraspecific aggression and reduced breeding success due to interference. This creates a conservation dilemma: management that inadvertently reduces predator pressure might allow for a less dense, more sustainable colony structure for cormorants, but could also encourage colony expansion that increases competition with gulls. The viability of these colonies is also tied to broader ecological conditions.

Like other nomadic larids in steppe regions, the presence of Palas's Gulls is highly dependent on unstable hydrological regimes and the availability of isolated islands, making them susceptible to cyclical drying of lakes (Barbazyuk 2020). Furthermore, our study site exists within a network of interconnected colonies. This means that the viability of the Kitay Island Palas's Gull colony is not only a local issue but is also influenced by management decisions and environmental pressures thousands of kilometers away. This is corroborated by research showing that human disturbance can exacerbate interspecific aggression, as observed in mixed colonies of cormorants and herons (Somers et al. 2011). On Kitay Island, the identification of core, densely packed cormorant breeding areas and the more widespread but sparser gull nesting zones provides a scientific basis for targeted management. Any future habitat modification, disturbance regulation, or predator control must account for these species-specific spatial configurations to avoid unintended collateral damage. For example, a disturbance event in a cormorant cluster would impact a vast number of nests simultaneously, whereas the same event might affect fewer gull nests but could be more disruptive to their sensitive territorial spacing.

Furthermore, the long-term viability of these colonies cannot be considered in isolation. The Palas's Gull population in the broader region, including the Sivash lagoons, may be subject to fluctuations influenced by climatic factors. Although the global Palas's Gull population is considered stable (BirdLife International 2018), local populations can be vulnerable. The dispersed nesting strategy of the gulls on Kitay Island, while reducing intraspecific conflict, may also make them more susceptible to localized predation or human disturbance across a wider area compared to the defensible clusters of cormorants. This vulnerability is compounded by the fact that in ground-nesting colonies, competition for space can be more intense and direct than in tree-nesting situations, as there is no three-dimensional structure to facilitate niche separation (Somers et al. 2011).

In conclusion, the spatially explicit approach of this study moves beyond simple nest counts to reveal the ecological structure of the Kitay Island bird community. The coexistence of Great Cormorants and Palas's Gull is facilitated by a spatial organization that reflects their innate breeding strategies, colonial clustering as a potentially predator-mediated, pro-active anti-predator strategy for cormorants, which can lead to higher nest densities and shorter NNDs (van Eerden & van Eerden 2022), and a dispersed, low-fidelity nesting pattern for the gull (Kharitonov

1999), and results in measurable segregation. Our results, supported by this framework, suggest that the clustered pattern of Great Cormorants is not a static feature but a dynamic adaptation, potentially influenced by interactions with other species as seen in mixed colonies (Lee et al. 2019). The quantification of NND provides a baseline for understanding how these species tolerate proximity, while the broader context of regional connectivity, climate vulnerability underscored by the species' nomadic nature in response to water levels (Barbazyuk 2020), and the documented vulnerability of the gull to interspecific competition and predation (Mierauskas & Buzun 1991; Panov 2009) underscores that local conservation is nested within a complex biogeographic and behavioral system.

These findings underscore that effective conservation planning for colonial waterbirds in the Sivash lagoon system must integrate an understanding of fine-scale spatial ecology, regional colony networks, climate resilience, and the behavioral drivers of colony structure, including the "ecology of fear" and interspecific interactions, to protect critical breeding habitats, minimize anthropogenic disturbance, and mitigate the impacts of environmental change on these ecologically important species.

Conclusions

Integrated spatial analysis reveals fundamentally distinct nesting patterns between Great Cormorant and Palas's Gull colonies on Kitay Island. Great Cormorants formed intensely clustered aggregations (mean NND = 0.23 m; Ripley's K, $p < 0.01$), consistent with colonial breeding. Conversely, Palas's Gull exhibited a dispersed, territorial distribution (mean NND = 0.67 m; random to regular Ripley's K).

Significant spatial segregation between the species, evidenced by a negative correlation in nest densities and cross-K function results, indicates niche partitioning that facilitates coexistence in a limited habitat.

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