

Hypothesis-Based Analysis of the Effects of Supplemental Feeding on the Wintering Space Use of Whooper Swans (*Cygnus cygnus*)

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Abstract: This study investigated the effects of supplemental feeding on the wintering spatial behavior of Whooper Swans (*Cygnus cygnus*) in South Korea by analyzing five spatial indicators: home range extent, spatial concentration, residence time, daily movement distance, and habitat use diversity. Using high-resolution Global Navigation Satellite System (GNSS) tracking data from two major sites—the Nakdong River Estuary (fed) and Junam Reservoir (unfed)—we examined how artificial feeding interacts with habitat structure and individual movement strategies. Contrary to the expectation that feeding reduces movement and increases site fidelity, swans in the fed estuary exhibited larger home ranges and shorter daily distances, but significantly lower habitat diversity. These results suggest that supplemental feeding improves energy efficiency while potentially promoting spatial fixation and ecological dependency, particularly in complex landscapes. The fed group showed fewer land cover types and lower Shannon diversity indices, indicating narrower habitat use and increased vulnerability to environmental changes or disease outbreaks. These findings emphasize the dual effects of feeding intervention and habitat heterogeneity on spatial behavior in migratory waterbirds. The results highlight the need for balanced wintering site management that accounts for both the energetic benefits and potential ecological risks of artificial feeding, with implications for conservation and disease prevention along the East Asian Flyway.

<https://doi.org/10.5338/KJEA.2025.44.32>

Agric. Environ. Sci. 2025, 44, 309-321

Received: August 1, 2025

Revised: August 25, 2025

Accepted: September 19, 2025

Published: September 26, 2025

Online ISSN: 2233-4173

Print ISSN: 1225-3537



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Keywords: Global navigation satellite system (GNSS) tracking, Home range extent, Movement ecology, Supplemental feeding

Introduction

The Whooper Swan (*Cygnus cygnus*) is a large migratory waterbird that breeds across the tundra regions of northern Eurasia and winters in parts of East Asia, Europe, and the Middle East [1]. In South Korea, the species is legally protected as Natural Monument No. 201 and designated as a Class II endangered wildlife species [2]. Major wintering sites in Korea include the Nakdong River Estuary, Junam Reservoir, and Upo Wetlands. The national wintering population, which was around 5,590 individuals in the 1990s, increased to approximately 39,000 in the early 2000s and has since remained relatively stable or shown a slight decline [3,4].

Among these sites, the Nakdong River Estuary is one of the most critical habitats, hosting approximately 20-26% of the national wintering population. Its complex landscape of river channels, mudflats, and freshwater wetlands provides key resources for foraging, roosting, and preparation for spring migration [5,6]. However, since the 1980s, rapid urban development and the construction of hydraulic infrastructure have significantly reduced natural habitats and food availability in the area [7]. In response, the local government began an artificial feeding program in 2008, providing approximately 50,000 kg of grains (primarily corn and sweet potatoes) each winter (November to February) at several sites, including the Eulsukdo Migratory Bird Park and Maekdo Ecological Park.

Although supplemental feeding is generally known to enhance winter survival and increase site fidelity, its ecological effects on home range, habitat dependence, and spatial behavior remain insufficiently understood [8]. Moreover, increased local density near feeding stations can elevate the risk of infectious disease transmission, such as highly pathogenic avian influenza (HPAI) [9]. Recent studies have shown that artificial feeding not only affects energy dynamics but also alters behavior and increases inter-individual contact, which may elevate the risk of disease transmission in birds [10,11]. Despite these concerns, few studies in Korea have quantitatively compared spatial behavior between fed and unfed Whooper Swan populations.

Understanding the spatial ecology of migratory birds is essential for species conservation, habitat management, disease control, and biodiversity policy development. Advances in GNSS-based telemetry now allow for high-resolution tracking at the individual level, leading to more detailed assessments of movement ecology and home range [12,13]. However, empirical evidence on the effects of artificial feeding on spatial behavior remains limited, particularly for large-bodied waterfowl such as the Whooper Swan.

This study aims to quantify the effects of supplemental feeding on the wintering home range and spatial use patterns of Whooper Swans, by comparing individuals from a feeding site (Nakdong Estuary) and a non-feeding site (Junam Reservoir). Using GNSS-based tracking data, we analyzed five spatial ecological indicators—home range size, spatial concentration, time spent near feeding areas, daily movement distance, and habitat use diversity. The results provide empirical insights into how feeding practices influence swan behavior and contribute to science-based winter habitat management and conservation planning for migratory waterbirds.

We tested five a priori hypotheses regarding how supplemental feeding alters winter spatial behavior: (H1) feeding reduces the overall home range extent (MCP, KDE 95/KDE 50); (H2) feeding increases spatial concentration within core areas (KDE 50/KDE 95); (H3) feeding increases residence time near feeding centers; (H4) feeding reduces movement distance; and (H5) feeding reduces habitat-use diversity (number of land-cover types and Shannon diversity). Details of the corresponding indicators and statistical tests are summarized in Table 1 (See the hypothesis-based analytical framework).

Table 1. Summary of hypotheses, predicted patterns, and key metrics used to evaluate the effects of supplemental feeding on the wintering spatial behavior of Whooper Swans (*Cygnus cygnus*)

Hypothesis	Description	Predicted pattern in the feeding group (Nakdong River)	Key analytical metrics
H1	Supplemental feeding reduces overall home range size.	Smaller MCP and KDE 95/50 areas.	MCP (100%), KDE (95%, 50%)
H2	Supplemental feeding increases spatial concentration.	Higher KDE50/KDE95 ratio.	KDE50/KDE95 ratio
H3	Supplemental feeding increases time spent near feeding centers.	Longer duration within 300m radius of feeding center.	Residence time within 300m (in hours)
H4	Supplemental feeding reduces daily movement distance.	Shorter average daily travel distance.	Daily movement distance (m/day)
H5	Supplemental feeding reduces habitat use diversity.	Fewer land cover types and lower Shannon diversity index.	Number of land cover types, Shannon diversity index

Note: Mann–Whitney U tests were applied for all statistical comparisons between the fed (Nakdong) and unfed (Junam) groups.

Table 2. Summary of Supplemental Feeding Protocols in the Nakdong River Estuary

Feeding Site	Coordinates	Feeding Time	Frequency	Feed Type	Amount per Feeding	Feeding Period
Eulsukdo Artificial Bird Habitat	35°05'33.40"N 128°56'08.97"E	09:00 AM	Daily	Sliced sweet potatoes	300 kg	November 2024 – February 2025
Eulsukdo Artificial Roost	35°05'16.83"N 128°56'27.64"E	09:30 AM	Daily	Sliced sweet potatoes	200 kg	November 2024 – February 2025
Maekdo Ecological Park	35°08'31.83"N 128°57'03.03"E	02:00 PM	5–6 times/ week	Sliced sweet potatoes	200 kg	November 2024 – February 2025

Results

Home range size (H1)

This result corresponds to Hypothesis 1 (H1) described in Table 2, which predicted that supplemental feeding reduces the overall home range extent of Whooper Swans. The total home range area (KDE 95%) and core area (KDE 50%) were significantly smaller in the Nakdong Estuary group (fed) than in the Junam Reservoir group (unfed). The average KDE 95% area was 2.82 km² for Nakdong and 6.48 km² for Junam, while the KDE 50% area averaged 0.62 km² and 1.87 km², respectively. Similarly, the MCP area showed a significant difference, with the Nakdong group averaging 5.43 km² and the Junam group 15.83 km² (Fig. 1 and 2). These results suggest that supplemental feeding is associated with smaller spatial ranges during the wintering period. All differences were statistically significant (Mann–Whitney U test, $p<0.05$).

Spatial concentration (H2)

Contrary to Hypothesis 2 (H2) in Table 1, spatial concentration within core areas (KDE 50/KDE 95) was lower at the fed site than at the unfed site (Nakdong: mean = 0.22; Junam: mean = 0.32; Fig. 3), and the difference was not statistically significant

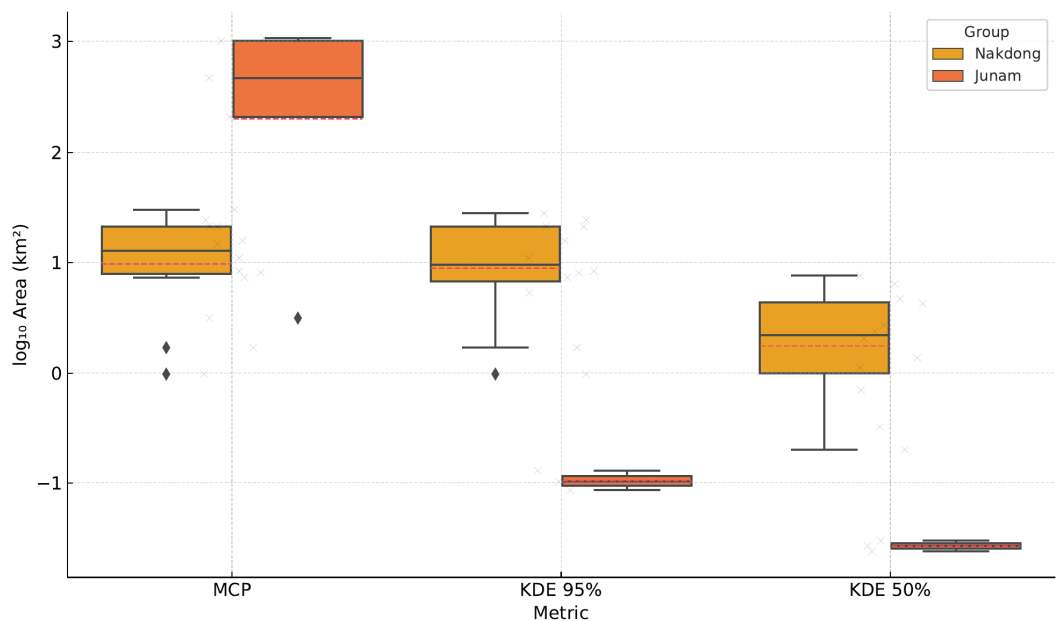


Fig. 1. Comparison of KDE 95%, KDE 50%, and MCP home range extents for Whooper Swans in the Nakdong Estuary (fed group) and Junam Reservoir (unfed group).

Bars represent group means; error bars indicate standard deviations.

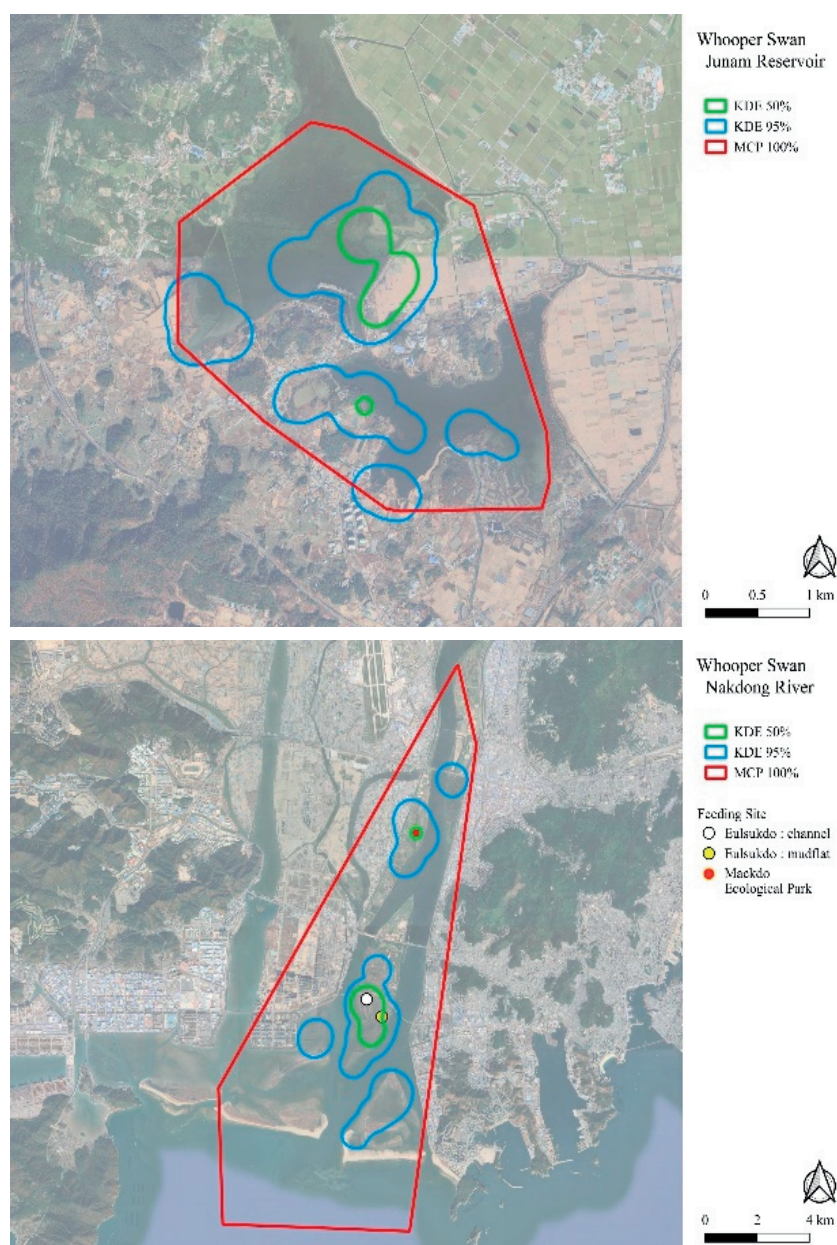


Fig. 2. Boxplots showing KDE 95%, KDE 50%, and MCP values for Whooper Swans by wintering site.

Each box represents the interquartile range (IQR), the line inside the box indicates the median, and whiskers denote minimum and maximum values excluding outliers.

(Mann-Whitney U test, $p=0.0747$). This pattern suggests a broader dispersion of core-area use at the fed site rather than stronger aggregation around feeding centers. Accordingly, we found no statistical support for H2 at the current sample size and spatial resolution.

Duration of stay (H3)

Duration of Stay (H3). Contrary to Hypothesis (H3) in Table 1, residence time at the wintering site was longer at the unfed site than at the fed site (Junam: mean = 186 days; Nakdong: mean = 86 days; Fig. 4). the between-site difference was statistically significant (Mann-Whitney U test, $p=0.0025$). Accordingly, H3 was not supported under the present sampling regime; instead, the unfed population exhibited greater site fidelity during the wintering season.

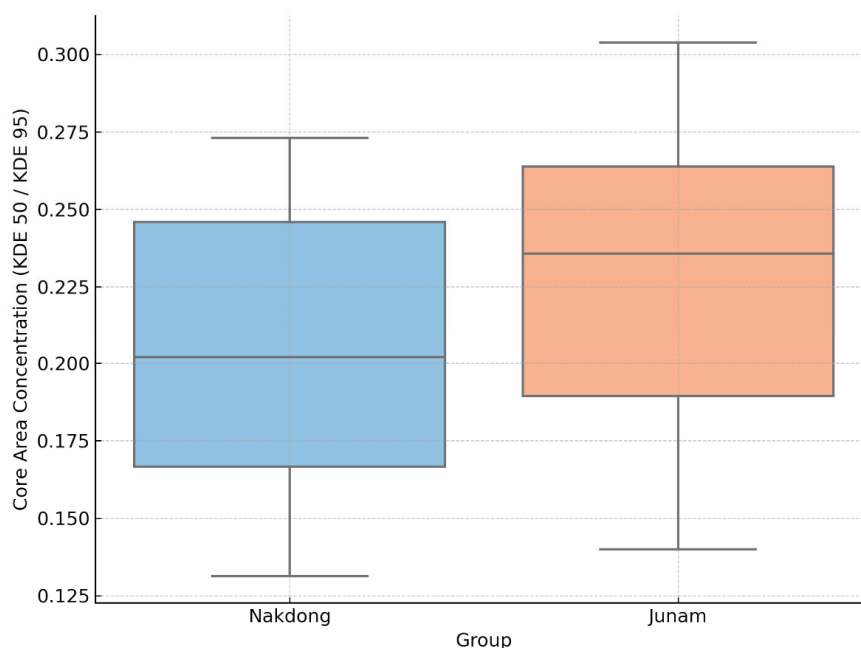


Fig. 3. Comparison of core area concentration (KDE 50 / KDE 95) between Whooper Swans in the Nakdong River Estuary (feeding site) and Junam Reservoir (non-feeding site).

Lower values indicate higher spatial concentration. Each point represents an individual swan.

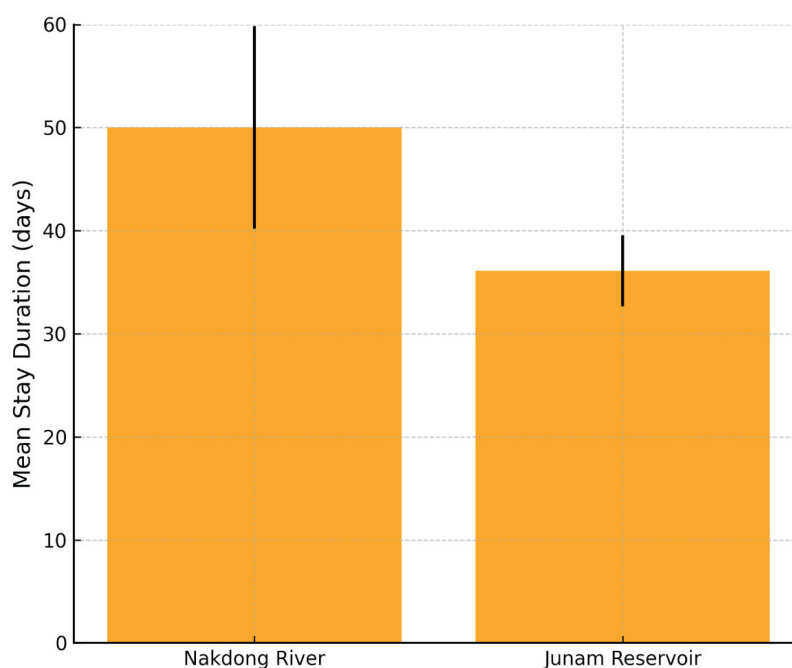


Fig. 4. Comparison of mean stay duration of Whooper Swans wintering in the Nakdong River and Junam Reservoir.

Bars represent means and error bars indicate standard deviations.

Daily movement distance (H4)

Daily Movement Distance (H4). Consistent with Hypothesis 4 (H4) in Table 1, daily movement distance was lower at the fed site than at the unfed site (Nakdong: mean = 1.47 km; Junam: mean = 3.25 km; Fig. 5), and the between-site difference

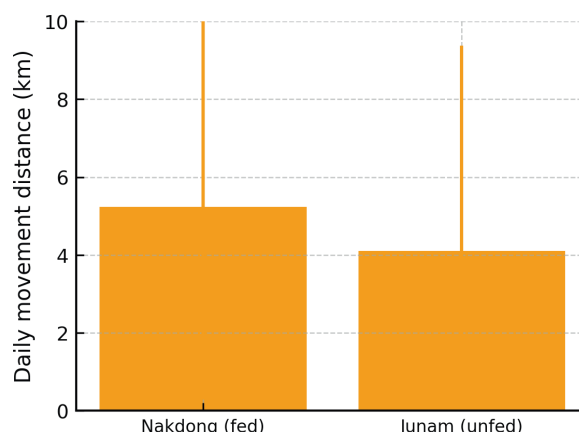


Fig. 5. Comparison of mean daily movement distances for Whooper Swans in the Nakdong Estuary (fed group) and Junam Reservoir (unfed group).

Bars represent group means; error bars indicate standard deviations.

was statistically significant (Mann-Whitney U test, $p=0.0263$). This patterns indicates that concentrated provisioning at the fed estuary reduced the need for daily travel during winter.

Habitat use diversity (H5)

Habitat-Use Diversity (H5). Consistent with Hypothesis 5 (H5) in Table 1, habitat-use diversity was lower at the fed site than at the unfed site. The unfed group (Junam) used more land-cover classes on average than the fed group (Nakdong) (Junam: 6.6 vs Nakdong: 4.4), and this difference was statistically significant (Mann-Whitney U test, $p=0.0039$; Fig. 6). Similarly, the Shannon diversity index was higher in the unfed group (1.19 vs 0.79), with a significant difference ($p=0.0034$; Fig. 7). In this context, higher numbers of land-cover classes and higher Shannon values indicate broader habitat use and greater ecological niche breadth, whereas lower values indicate spatial restriction and homogenization. Take together, these results support H5, showing reduces habitat-use diversity in the fed population during winter.

Discussion

This study quantitatively evaluated the effects of supplemental feeding on the spatial behavior of wintering Whooper Swans (*C. cygnus*) by testing five a priori hypotheses across five key spatial dimensions-home range extent, spatial concentration, residence time, daily movement distance, and habitat-use diversity. Our results show that feeding effects are context dependent, varying with habitat structure, hydrological density, and site connectivity rather than exerting a uniform influence across sites [8,14]. Consistent with H4 and H5, feeding reduced daily movement distance and habitat-use diversity, whereas H2 (greater core-area concentration at the fed site) was not supported and H3 (longer residence time near feeding centers) was contradicted. Our interpretations explicitly integrate measurement choice (MCP vs KDE), hydrological structure, and site-specific habitat connectivity to avoid over-attributing effects to feeding alone.

Contrary to previous reports that feeding typically reduces winter home range extent and increases site fidelity [8,14], Whooper Swans at the Nakdong River Estuary exhibited greater home range extent (MCP 100%) and more dispersed core areas (KDE 95 and KDE 50) than those at Junam Reservoir. We attribute this discrepancy to the heterogeneous and highly connected habitat matrix of the Nakdong River Estuary, including diverse wetlands, tidal flats, and ecological parks such as Eulsukdo and Maekdo [15-17]. In particular, high hydrological density and spatial connectivity likely promoted broad-area exploration, which

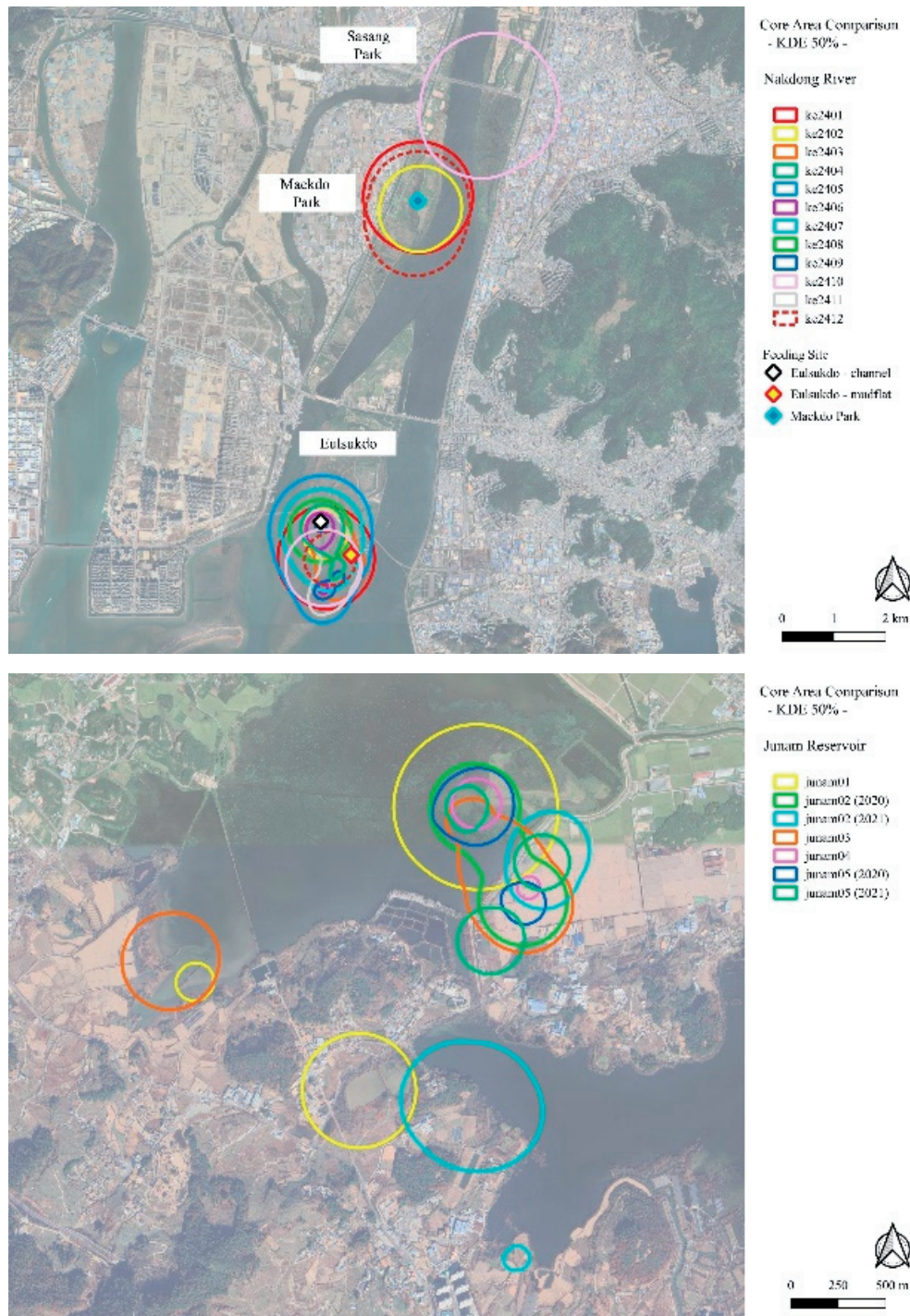


Fig. 6. Comparison of home range core areas (KDE 50%) of Whooper Swans in the Nakdong River Estuary (left panel) and Junam Reservoir (right panel).

can offset feeding-induced anchoring. Moreover, MCP estimates are sensitive to irregular excursions and outliers [18,19]. For instance, individuals such as ke2404 and ke2410, although centered around feeding sites, occasionally exhibited long-range excursions. By contrast, the relatively confined freshwater setting and lower hydrological complexity at Junam appeared to constrain movement naturally [6]. Taken together, these observations indicate that feeding effects on home range extent must be interpreted in conjunction with habit structure, connectivity, and environmental constraints [8,14].

Spatial concentration, measured as KDE 50/KDE 95, was lower at the fed site (Nakdong) than at the unfed site (Junam),

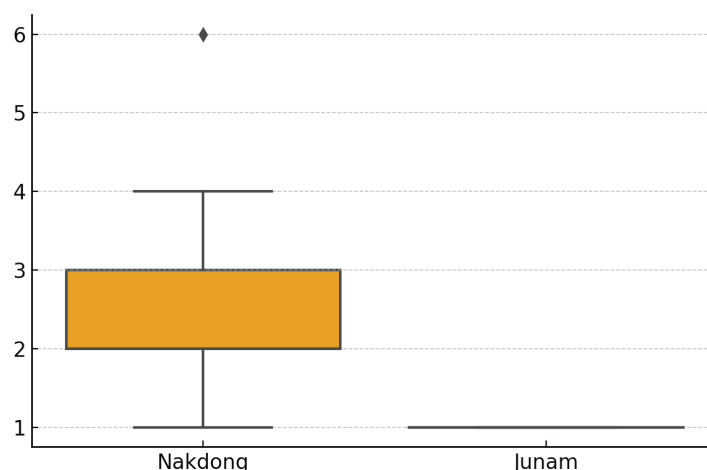


Fig. 7. Comparison of regional diversity of space use in Whooper Swans between fed (Nakdong) and unfed (Junam) groups.

and the difference was not statistically significant. Although higher concentration at feeding site has been reported elsewhere [8,14,15], our non-significant pattern likely reflects landscape openness, hydrological heterogeneity, and population-level movement tendencies that diffuse core use [5,16,20]. Thus, spatial concentration is not driven by feeding alone, but also by the physical layout and ecological variability of wintering grounds.

Residence time was significantly longer at Junam Reservoir than at the Nakdong River Estuary, contradicting H3 and challenging the expectation that feeding prolongs site use [8,14]. We infer that spatial confinement and habitat simplicity at Junam encourage longer stays, whereas the extensive, well-connected estuarine mosaic at Nakdong facilitates mobility even when provisioning is present [6,7,13]. This underscores that residence patterns can be more strongly governed by habitat characteristics than by feeding per se [21].

Daily movement distances were significantly shorter in the Nakdong population, consistent with H4 and with the interpretation that concentrated resources reduce foraging travel [8,14]. This effect is likely reinforced by the dense, patchy wetland structure at Nakdong, which enables localized movements while maintaining resource access [20]. Conversely, the lack of feeding and lower ecological complexity at Junam likely forced broader exploration to secure resources, thereby increasing daily range [13].

Regarding habitat-use diversity, the fed population at Nakdong used fewer land-cover classes (mean ≈ 4.4) and had a lower Shannon index (≈ 0.79) than the unfed population at Junam (≈ 6.6 classes; Shannon ≈ 1.19), with significant differences for both metrics. These results support H5, indicating that provisioning can narrow niche breadth and homogenize space use [10,11]. While reduces diversity may enhance short-term foraging efficiency, it can also elevate ecological risk by increasing exposure to localized threats and dampening behavioral flexibility [9,22].

Given ethical and permitting constraints on capture and tagging, our individual-level inferences should be interpreted with appropriate caution; nevertheless, consistent effect directions across multiple indicators and sites provide convergent evidence for context-dependent feeding effects.

Inter-metric correlations (Table S1) clarify how changes in home range extent co-vary with core-area concentration, daily distances, and habitat-use diversity, reinforcing a landscape-informed view of effects.

In summary, supplemental feeding had measurable effects across multiple spatial dimensions, but these effects were modulated by ecological context especially hydrological structure, habitat diversity, and connectivity. Accordingly, management should move beyond a simple feeding-non-feeding dichotomy and adopt a landscape-based approach that integrates regional ecological characteristics, population health, and disease preparedness [14,21,22]. This is particularly pertinent given evidence that provisioning can increase inter-individual contact and alter movement strategies in way that affect both energy dynamics and disease transmission [10,11].

Materials and Methods

Study area

The primary study site was the Nakdong River Estuary, located in southeastern South Korea, encompassing approximately 87.28 km². Recognized as one of the largest and most ecologically important wintering grounds for migratory waterbirds in the country, the estuary was designated as Natural Monument No. 179 in 1966 [23], registered under the East Asian–Australasian Flyway Partnership (EAAFP) in 2009, and acknowledged as an Important Bird and Biodiversity Area (IBA) by BirdLife International.

During the wintering period (November to February), supplemental feeding is carried out at three designated locations within the estuary: Eulsukdo Migratory Bird Park, the southern tidal flat of Eulsukdo, and Maekdo Ecological Park. At these sites, sweet potato strips are provided at fixed times and frequencies, with a total annual supply volume of approximately 50,000 kg. For reproducibility, operational details of the feeding stations—including precise coordinates, feeding times and frequencies, feed type, and per-event amounts—are summarized in Table 2 (locations illustrated in Fig. 8). These feeding practices primarily target Whooper Swans (*C. cygnus*), although other waterfowl species such as ducks and geese also forage at the same locations.

The sex of the GPS-tagged swans was not determined, as sexing procedures were intentionally excluded to minimize handling time and stress during transmitter deployment, in line with ethical standards for wildlife research.

As a control site, Junam Reservoir in Changwon, southeastern Korea, is a natural freshwater wetland of approximately 6.02 km² area. Shallow water and rich aquatic vegetation support wintering swans and other waterbirds, with winter counts showing between 12,000–14,000 individuals representing 60–65 species [24]. In contrast to the Nakdong Estuary, Junam receives no artificial feeding and thus represents a baseline condition of natural foraging and movement. Its shallow water and diverse aquatic vegetation provide suitable habitats for wintering swans and other waterbirds [25] (Fig. 8 and 9).

GNSS tracking and data collection

From December 2024 to March 2025, Global Navigation Satellite System (GNSS)-based tracking was conducted on 12 Whooper Swans at the Nakdong River Estuary (supplemental feeding site) and 5 individuals at the Junam Reservoir (non-feeding control site). On 17 December 2024, twelve adult swans were captured near Eulsukdo using a cannon net. Each bird was fitted with a GNSS transmitter (WT-300, KoEco, Republic of Korea; approximately 65 g, less than 1% of body weight) using a backpack harness. The tagging procedure followed the protocol of [26] and was completed within five minutes to minimize handling stress. All individuals were immediately released at the capture site.

Location data were recorded at one-hour intervals and transmitted twice daily (09:00 and 16:00) to a remote server via cellular networks. To ensure data accuracy, location points with a Dilution of Precision (DOP) value greater than 5 were excluded from the dataset [27]. Additional filtering removed coordinates with biologically implausible values, such as instantaneous speeds exceeding 100 km/h. Erroneous points with positional errors exceeding 100 m or abrupt long-distance displacements (>30 km) were also removed during preprocessing.

Sample sizes were constrained by ethical considerations and permitting requirements for capturing a nationally protected species (Permit No. 2025-30), as well as the need to minimize handling time and device load. Although modest, our sample sizes fall within the range waterbirds and adequate for hypothesis-driving comparisons when interpreted with appropriate caution [12,13,19,26].

Home range and spatial analysis

We analyzed the winter home ranges and pre-migratory inland shifts of Whooper Swans using GNSS tracking data. Spatial analyses were conducted using QGIS (version 3.34.x) and R (version 4.x) to evaluate individual movement extents, core-use

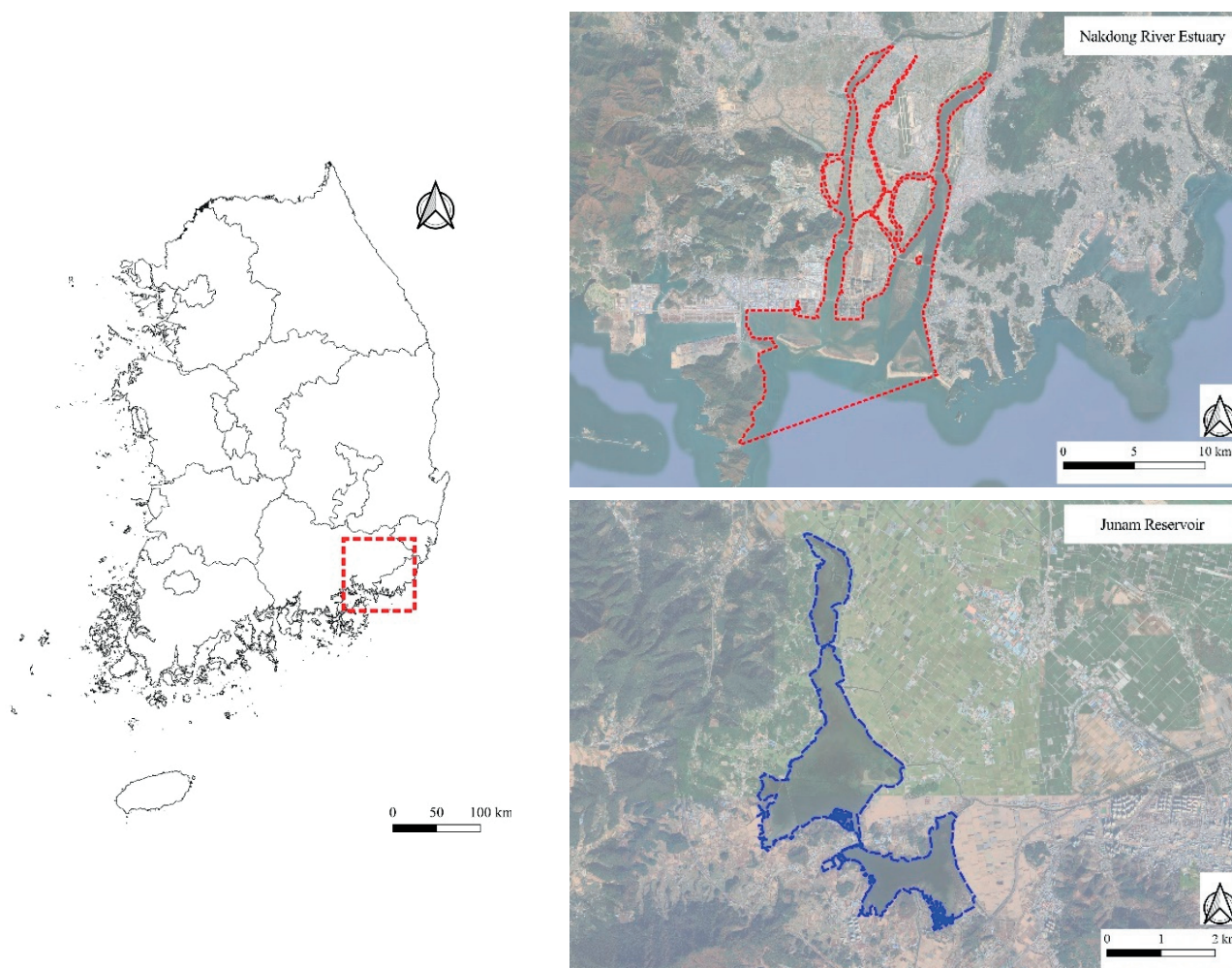


Fig. 8. Location of Study Area – Sanctuary of Migratory Birds at Nakdong River Estuary and Junam Reservoir.



Fig. 9. Artificial feeding sites in the Nakdong River Estuary (a–c) and the non-feeding control site at Junam Reservoir (d).

areas, inland dispersal prior to northward migration, and stopover-site use [28]. All computations used the quality-controlled hourly fixes described in GNSS tracking and data collection section.

Home range estimation. Home ranges were estimated using the Minimum Convex Polygon (MCP, 100%) and Kernel Density Estimation (KDE, 95% and 50%) methods. MCP delineated the overall movement extent, whereas KDE 95 represented broadly used areas and KDE 50 identify core-use areas [19,29]. Seasonal differences in space use and spatial concentration were evaluated by comparing MCP, KDE 95, and KDE 50 across winter periods.

Spatial indicators. To enable hypothesis-driven comparisons, we defined five spatial indicators that directly map to H1-H5:

- (i) home range extent (MCP, KDE 95, and KDE 50);
- (ii) spatial concentration (the ratio KDE 50/KDE 95, with higher values indicating stronger core-area concentration);
- (iii) residence time (total hours from hourly GNSS fixes occurring within the wintering utilization distribution during the study period);
- (iv) daily movement distance (sum of step lengths between consecutive 1-h fixes after filtering); and
- (v) habitat-use diversity (the number of land-cover classes used and the Shannon diversity index, computed from the proportions of fixes in each class).

Stopover definition and metrics. Stopover sites were defined as areas where individuals remained within a 3 km radius for more than 48 consecutive hours [30,31]. For each stopover event, we calculated the duration of stay, centroid coordinates, and KDE area.

Pre-migratory inland shifts. Pre-migratory inland shift strategies were categorized following the classification framework proposed by [13], and were interpreted in conjunction with the above spatial indicators to contextualize site-specific movement behaviors.

Statistical analysis

To examine group differences in key spatial metrics—including home range extent (MCP and KDE), spatial concentration (KDE 50/KDE 95), residence time, daily movement distance, and habitat-use diversity—we first tested for normality using the Shapiro–Wilk test and for homogeneity of variance using Levene’s test. Based on these diagnostics, either independent sample *t*-tests (Welch’s correction applied when variances were unequal) or Mann–Whitney *U* tests were conducted. All tests were two-tailed with the significance level set at $\alpha=0.05$. Following [32], we controlled the false discovery rate (FDR) and, where multiple related tests were conducted within an indicator family, *p*-values were adjusted using the Benjamini–Hochberg procedure [32].

To compare multivariate patterns of space use, we applied Permutational Multivariate Analysis of Variance (PERMANOVA) using the *vegan* package in R with 999 permutations. Prior to analysis, variables were z-standardized to ensure comparability across metrics, and Euclidean distance was used as the dissimilarity measure.

In addition, to evaluate inter-metric relationships, we computed Spearman’s rank correlations among key spatial indicators (MCP, KDE 95, KDE 50, KDE 50/KDE 95, daily movement distance, and Shannon diversity). For these correlations, Benjamini–Hochberg FDR adjustments were applied to control for multiple testing [32]. Summary statistics (ρ and adjusted *p*) are provided in Table S1 (Supplementary Material).

All statistical analyses were performed using R (version 4.2.0) and QGIS (version 3.28.4).

Hypothesis-based analytical framework

To evaluate the effects of supplemental feeding on the winter home range and spatial use patterns of Whooper Swans, we developed five specific hypotheses (H1–H5). Each hypothesis was paired with relevant spatial metrics and corresponding statistical tests. These hypotheses are summarized in Table 1.

Each hypothesis was designed to comprehensively assess a key aspect of spatial use (range size, concentration, duration of

stay, movement distance, and habitat diversity) in relation to supplemental feeding. Appropriate statistical comparisons, including t-tests or non-parametric alternatives, were applied to each hypothesis. We acknowledge the limitations posed by the relatively small sample size and have taken this into account in the interpretation of results.

Summary of Hypotheses, predicted patterns, and key metrics used to evaluate the affects of supplemental feeding on the wintering spatial behavior of Whooper Swans (*C. cygnus*).

Data Availability: All data are available in the main text or in the Supplementary Information.

Author Contributions: The authors express their sincere gratitude to S.Lee, H.Cho, H.Lee, Y.Cho for their valuable support in the conduct of this study.

Notes: The authors declare no conflict of interest.

Acknowledgments: This research was supported by Chungnam National University through its funding program for education, research, and student guidance.

The 12 Whooper Swans used in this research were captured under official permission granted by the Korea Heritage Service (Permit No. 2025-30), as the species is designated as nationally protected in Korea.

Additional Information:

Supplementary information The online version contains supplementary material available at <https://doi.org/10.5338/KJEA.2025.44.32>

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Peer review information Agricultural and Environmental Sciences thanks the anonymous reviewers for their contribution to the peer review of this work.

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References

1. Delany S, Scott D, Helmink ATF (2006) Waterbird Population Estimates – Fourth Edition. Wetlands International.
2. Culture Heritage Administration (2020) Natural Monument Scenic Site.
3. Choi JE, Kim JY, Do Y, Joo G-J (2018) Population trends of wintering Whooper Swans (*Cygnus cygnus*) in South Korea: Data from the Winter Waterbird Census Program. Korean Journal of Ecology and Environment, 51(4), 365–372. <https://doi.org/10.11614/KJEE.218.51.4.365>.
4. Wetlands International (2018) Guidance on waterbird monitoring methodology: Field protocol for waterbird counting. Wetlands International.
5. Lee Y, Do Y, Suh SO, Jang J-D, Lee C, Joo G-J (2025) Distribution and habitat use of wintering waterbirds in Busan and Gyeongsangnam-do. Korean Journal of Ecology and Environment, 58(1), 61-69.
6. Lee JN, Lee WH, Kim MG, Park GS (2022) A study on the wintering distribution of the Whooper Swan (*Cygnus cygnus*) within the lower Nakdong River, Busan city. Journal of People, Plants, and Environment, 25(5), 457-474. <https://doi.org/10.11628/ksppe.2022.25.5.457>.
7. Hong SH (2020) Relationship between population of wintering Whooper Swan (*Cygnus cygnus*) and bridge spacing in the lower Nakdong River, Korea. Korean Journal of Environment and Ecology, 34(3), 191-197.
8. Oro D, Genovart M, Tavecchia G, Fowler MS, Martínez-Abraín A (2013) Ecological and evolutionary implications of food subsidies from humans. Ecology Letters, 16(12), 1501-1514. <https://doi.org/10.1111/ele.12187>.
9. Newman SH, Hill NJ, Spragens KA, Janies D, Voronkin IO, Prosser DJ, Yan B, Lei F, Batbayar N, et al. (2012) Eco-virological approach for assessing the role of wild birds in the spread of avian influenza H5N1 along the Central Asian Flyway. PLoS ONE, 7(2), e30636. <https://doi.org/10.1371/journal.pone.0030636>.
10. Miranda-Cavallieri M, Allendes-Muñoz C, Matus-Olivares C, Lisón F (2023) Habitat preference and abundance of *Coscoroba coscoroba* and *Cygnus melancoryphus* in Petrel wetland (O'Higgins region, Chile): Implications in the conservation. Gayana, 87(1), 86-96. <https://doi.org/10.4067/S0717-65382023000100086>.

11. Allendes-Muñoz C, Miranda-Cavallieri M, Matus-Olivares C, Lisón F (2023) Behaviour patterns of South American swans and potential ecosystem services supplied to salt production systems. *Gayana*, 87(2), 97-107. <https://doi.org/10.4067/S0717-65382023000200097>.
12. Shimada T, Yamaguchi NM, Hijikata N, Hiraoka E, Hupp JW, Flint PL, Tokita K, Fujita G, Uchida K, et al. (2014) Satellite tracking of migrating Whooper Swans (*Cygnus cygnus*) wintering in Japan. *Ornithological Science*, 13(2), 67-75. <https://doi.org/10.2326/osj.13.67>.
13. Yan H, Ma X, Yang W, Xu F (2024) Multi-scale habitat selection by the wintering Whooper Swan (*Cygnus cygnus*) in Manas National Wetland Park, Northwestern China. *Diversity*, 16(5), 306. <https://doi.org/10.3390/d16050306>.
14. Fox AD, Jónsson JE, Aarvak T, Bregnballe T, Christensen TK, Clausen KK, Clausen P, Dalby L, Holm TE, et al. (2015) Current and potential threats to Nordic duck populations — a horizon scanning exercise. *Annales Zoologici Fennici*, 52(4), 193-220. <https://doi.org/10.5735/086.052.0401>.
15. Chisholm H, Spray, C (2002) Habitat usage and field choice by Mute and Whooper Swans in the Tweed Valley, Scotland. *Waterbirds: The International Journal of Waterbird Biology*, 25(S1), 177-182.
16. Elmberg J, Nummi P, Pöysä H, Sjöberg K (2006) Relationships between species richness, feeding guilds and habitat types in boreal wetland bird communities. *Oecologia*, 148(1), 141-150. <https://doi.org/10.1007/s00442-005-0378-2>.
17. Arzel C, Elmberg J, Guillemain M (2006) Ecology of spring-migrating Anatidae: A review. *Journal of Ornithology*, 147(2), 167-184. <https://doi.org/10.1007/s10336-006-0064-3>.
18. Harris S, Cresswell WJ, Forde PG, Trehwella WJ, Woollard T, Wray S (1990) Home-range analysis using radio-tracking data: A review of problems and techniques particularly as applied to the study of mammals. *Mammal Review*, 20(2-3), 97-123. <https://doi.org/10.1111/j.1365-2907.1990.tb00106.x>.
19. Seaman DE, Millspaugh JJ, Kernohan BJ, Brundige GC, Raedeke KJ, Gitzen RA (1999) Effects of sample size on kernel home range estimates. *Journal of Wildlife Management*, 63(2), 739-747.
20. Nolet BA (2006) Speed of spring migration of tundra swans *Cygnus columbianus* in accordance with income or capital breeding strategy. *Ardea*, 94, 579-591.
21. Sutherland WJ, Newton I, Green RE (Eds.) (2004) *Bird Ecology and Conservation: A Handbook of Techniques*. Oxford University Press, Oxford & New York.
22. Prosser DJ, Cui P, Takekawa JY, Tang M, Hou Y, Collins BM, Yan B, Hill NJ, Li T, et al. (2011) Wild bird migration across the Qinghai-Tibetan Plateau: A transmission route for highly pathogenic H5N1. *PLoS ONE*, 6(3), e17622. <https://doi.org/10.1371/journal.pone.0017622>.
23. Kim IK, Lee HS, Paek WK, Lee JW, Choi YB (2005) A study on the avifauna and waterbird populations of Nakdong River Estuary, South Korea. *Korean Journal of Ornithology*, 11(2), 55-70.
24. Jin S-D, Yu J-P, Choi J-S, Paik I-H, Kim I-K, Hong G-P, Cho H-J, Shin Y-U, Kang C-W (2012) Community characteristics of waterbirds in Junam Reservoir, Changwon-si, Korea. *Journal of Korean Nature*, 5(1), 43-50.
25. Lee SD, Kim H, Cho BG, Lee GG (2021) Characteristics and management plan for the distribution of *Nelumbo nucifera* community in Junam Wetland. *Journal of People, Plants and Environment*, 24(5), 469-483.
26. Kenward RE, Clarke RT, Hodder KT, Walls SS (2001) Density and linkage estimators of home range: Nearest-neighbor clustering defines multinuclear cores. *Ecology*, 82(7), 1905-1920.
27. Tahsin M, Sultana S, Reza T, Hossam-E-Haider M (2015) Analysis of DOP and its preciseness in GNSS position estimation. *Proceedings of the 2015 International Conference on Electrical Engineering and Information Communication Technology (ICEEICT)*, 1-6. <https://doi.org/10.1109/ICEEICT.2015.7307471>.
28. Kauhala K, Auttila M (2010) Estimating habitat selection of badgers—A test between different methods. *Folia Zoologica*, 59(1), 16-25.
29. Murphy EC, Dowding JE (1995) Ecology of the stoat in Nothofagus forest: Home range, habitat use and diet at different stages of the beech mast cycle. *New Zealand Journal of Ecology*, 19, 97-109.
30. Nuijten RJM, Kölzsch A, Van Gils JA, Hoyer BJ, Oosterbeek K, De Vries PP, Klaassen M, Nolet BA (2014) The exception to the rule: Retreating ice front makes Bewick's swans *Cygnus columbianus bewickii* migrate slower in spring than in autumn. *Journal of Avian Biology*, 45(2), 113-122. <https://doi.org/10.1111/j.1600-048X.2013.00287.x>.
31. Lee J-Y, Nam H-K, Park J-Y, Kang S-G, Batbayar N, Kim D-W, Hwang J-W, Tsend O, Natsagdorj T, et al. (2023) Migration routes and differences in migration strategies of Whooper Swans between spring and autumn. *Avian Research*, 14, 100113. <https://doi.org/10.1016/j.avrs.2023.100113>.
32. Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: Practical and powerful approach to multiple testing. *Journal the Royal Statistical society Series B (Methodological)*, 57(1), 289-300. <http://doi.org/10.1111/j.2517-6161.1995.tb02031.x>.