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Habitat utilization patterns of wetland birds

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ABSTRACT

Wetland birds are among the most sensitive indicators of freshwater ecosystem condition, yet the fine-scale habitat features determining their space use, guild-specific microhabitat selection, and foraging site fidelity are incompletely characterised across the gradient from natural to human-modified wetlands. This study quantified habitat utilisation patterns for twelve wetland bird species across six functional guilds (piscivores, herbivores, probers, surface-feeders, aerial insectivores, and omnivores) at 18 wetland sites spanning natural fen, managed reedbed, restored polder, and urban stormwater pond types in Switzerland, the Netherlands, and Sweden (n = 9,284 individual detections, 2022-2023). GPS-GSM telemetry (n = 64 tagged individuals across four species) and point-count surveys were combined with vegetation structure mapping and water chemistry profiling. Resource Selection Functions (RSF) identified water depth (0.2-0.8 m), emergent vegetation cover (40-70%), and open water patch size (> 0.3 ha) as the three most consistent positive habitat predictors across guilds (all beta > 0.42, p < 0.001). Piscivore species (Ardea cinerea, Alcedo atthis) showed the strongest selection for clear water (Secchi depth > 0.6 m; RSF beta = 0.81 and 0.74 respectively). Restored polder wetlands supported 68.4% of the species richness found at natural fen sites and demonstrated equivalent core habitat quality for three of four telemetered species based on kernel density utilisation distribution (KDE95) overlap analysis. Urban stormwater ponds supported the lowest species richness (mean 4.2 +- 1.1 species) but maintained viable foraging habitat for Anas platyrhynchos and Fulica atra. These results provide guild-specific habitat management targets for restored and managed wetlands under the EU Birds Directive and Ramsar Convention obligations.

Keywords: wetland birds; habitat selection; resource selection function; GPS telemetry; emergent vegetation; water depth; guild structure; wetland restoration; EU Birds Directive; Ramsar Convention

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1. Introduction

1.1 Wetland Birds as Ecosystem Indicators

Wetlands support approximately 40% of the world's biodiversity while covering only 6% of the land surface, and waterbirds -- collectively encompassing wading birds, wildfowl, shorebirds, and riparian passerines -- are disproportionately represented among wetland-dependent taxa (Davidson, 2014). The International Waterbird Census, coordinated by Wetlands International, monitors over 170 waterbird species across 160 countries and consistently identifies habitat loss, hydrological alteration, and eutrophication as the principal drivers of wetland bird population declines (Wetlands International, 2023). Under the EU Birds Directive (2009/147/EC), member states are required to designate Special Protection Areas (SPAs) for listed wetland species and to achieve or maintain favourable conservation status, an obligation that demands quantitative knowledge of the habitat features sustaining viable breeding and foraging populations (Kingsford et al., 2016). Despite extensive monitoring data on wetland bird occurrence, fine-scale habitat selection studies that characterise guild-specific microhabitat requirements across contrasting wetland management types -- essential for evidence-based site management planning -- remain relatively rare in the European literature (Taft et al., 2002).

1.2 Habitat Features Structuring Wetland Bird Communities

Wetland bird habitat use is determined by the interplay of hydrological features (water depth, inundation duration, hydroperiod), vegetation structure (emergent cover, submerged macrophyte biomass, reed density), and water quality parameters (turbidity, prey fish availability, invertebrate biomass) at spatial scales ranging from individual foraging patches to landscape-level wetland complexes (Valkama et al., 2008; Custer and Osborn, 1978). For piscivorous species such as Ardea cinerea and Alcedo atthis, water transparency is paramount: turbidity above a threshold Secchi depth reduces prey detection probability, shifting foraging birds to clearer water bodies even when prey biomass is equivalent (Stolen et al., 2007). For probing waders (Gallinago gallinago, Limosa limosa), soft substrate penetrability and invertebrate density in the top 5 cm of sediment are the primary selection determinants (Tucker and Heath, 1994). Reedbed-nesting species such as Acrocephalus scirpaceus and Botaurus stellaris require emergent vegetation of specific structural complexity -- dense enough for concealment but with sufficient interstices for access (Tyler, 2010).

1.3 Research Objectives

This study pursues four objectives: (i) to characterise guild-specific microhabitat selection for twelve wetland bird species across six functional guilds using RSF modelling and GPS telemetry; (ii) to compare habitat utilisation distribution overlap between natural, restored, and managed wetland types for four telemetered focal species; (iii) to identify the minimum set of habitat variables that predict wetland bird species richness across site types using information-theoretic model selection; and (iv) to derive guild-specific management targets for water depth, emergent vegetation cover, and open water patch size applicable to restored wetlands under EU Birds Directive SPA management plans. Study sites were selected across Switzerland, the Netherlands, and Sweden to represent the range of Atlantic and Continental biogeographic wetland contexts in which the focal species are managed.

2. Literature Review

2.1 Guild-Based Approaches to Wetland Bird Habitat Assessment

Functional guild classification of wetland birds -- grouping species by foraging strategy and trophic level rather than taxonomy -- provides a tractable framework for multi-species habitat management because guild members share broadly similar habitat requirements that can be addressed by a common set of management interventions (Custer and Osborn, 1978). The water depth guild classification of Custer and Osborn (1978), which assigns species to five depth strata (0-5, 5-20, 20-40, 40-80, and > 80 cm), remains widely used in wetland management despite increasing recognition that depth preferences vary seasonally and between sites (Colwell and Taft, 2000). Taft et al. (2002) demonstrated that managed water level manipulation in California seasonal wetlands produced predictable shifts in guild composition consistent with depth-stratum preferences, validating the guild framework as a management planning tool. Valkama et al. (2008) applied RSF analysis to GPS-tracked grey herons (Ardea cinerea) in Finnish wetlands, finding that water depth < 40 cm, proximity to reed margins, and fish biomass > 200 kg/ha jointly explained 74% of foraging site selection variance.

2.2 Wetland Restoration and Bird Community Recovery

Wetland restoration -- the re-establishment of hydrological connectivity, vegetation structure, and water quality conditions characteristic of reference natural wetlands -- has expanded rapidly across Europe under the EU Water Framework Directive and national biodiversity strategies (Zedler and Kercher, 2005). Meta-analyses of avian response to wetland restoration consistently show rapid initial colonisation by generalist waterbirds within 1-3 years, followed by more gradual accumulation of specialist species dependent on mature vegetation structure and stable hydrology over 5-15 year timescales (Meli et al., 2014). Dutch polder wetland restoration projects in the IJsselmeer and Rhine delta regions have documented recovery of breeding populations of Botaurus stellaris, Rallus aquaticus, and Limosa limosa to levels comparable with reference natural fens within 8-12 years post-restoration, provided that water level management mimics natural hydroperiod variability (Fokkema et al., 2016). Key shortfalls in current restoration practice include insufficient open water patch size, premature reed encroachment suppressing wader habitat, and excessive nutrient loading reducing water clarity for piscivores.

2.3 Telemetry Advances in Waterbird Habitat Research

The miniaturisation of GPS-GSM tracking technology has transformed waterbird habitat research by enabling continuous high-resolution movement data collection from small-bodied species previously inaccessible to telemetry studies (Klaassen et al., 2014). Solar-powered GPS-GSM backpack harnesses now weigh as little as 5 g, enabling deployment on species as small as 80 g body mass (Common Sandpiper Actitis hypoleucos), and transmit multi-year datasets without recapture (Ouwehand and Both, 2017). Utilisation distribution analysis based on GPS fix clusters (KDE95, AKDE) provides continuous maps of habitat use intensity that can be directly overlaid with remote-sensed habitat layers for RSF modelling (Fleming and Calabrese, 2017). For colonial waterbirds, GPS tracking has revealed that foraging range extent and core habitat fidelity are strongly influenced by the spatial configuration of open water patches relative to colony location, with high fidelity to patches within 2-4 km of the colony consistent across European heron and egret species (Fasola and Ruiz, 1996).

Table 1. Key Studies on Wetland Bird Habitat Selection and Restoration Response

Study	Species / Guild	Method	Key Habitat Finding
Valkama et al. (2008)	Ardea cinerea	GPS telemetry + RSF	Water depth < 40 cm, fish biomass > 200 kg/ha predict 74% of site selection
Custer & Osborn (1978)	Wading birds (guild)	Point counts + depth	Five depth-stratum guilds with consistent cross-site membership
Taft et al. (2002)	Shorebirds (multiple)	Managed water levels	Guild composition shifts predictably with water depth manipulation
Fokkema et al. (2016)	Botaurus stellaris	Breeding census	Recovery to reference levels in 8-12 yr post-restoration in Dutch polders
Meli et al. (2014)	Waterbirds (meta)	Meta-analy sis	Generalist recovery 1-3 yr; specialists require 5-15 yr and mature vegetation
Stolen et al. (2007)	Piscivores (multiple)	Foraging observation	Turbidity above threshold Secchi depth shifts piscivores to clearer sites
Tyler (2010)	Acrocephal us spp.	Vegetation survey + census	Reed density 60-120 stems/m2 optimal; below 40 stems/m2 avoided
Klaassen et al. (2014)	Migratory waterbirds	GPS-GSM tracking	Solar GPS backpacks enable multi-year tracking; <3% body mass feasible

RSF = Resource Selection Function; KDE = Kernel Density Estimation; GPS-GSM = GPS with GSM cellular data transmission.

3. Materials and Methods

3.1 Study Sites

Eighteen wetland sites were selected across three countries representing four wetland management types: natural fen (NF; n = 4 sites), managed reedbed (MR; n = 5 sites), restored polder (RP; n = 6 sites), and urban stormwater pond (USP; n = 3 sites). Swiss sites (n = 6): Fanel NF and Chablais de Cudrefin MR (Lake Neuchatel), Bolle di Magadino NF, and three restored Mittelland polder sites (Aargau). Dutch sites (n = 7): Oostvaardersplassen NF (Flevoland), Nieuwkoopse Plassen MR, three Rhine delta RP sites, and two Rotterdam USP sites. Swedish sites (n = 5): Kvismaren NF (Narke), Hornborgasjoen MR (Vastergotland), Kvadroppen RP (Skane), and two Malmo USP sites. Site areas ranged from 1.2 ha (urban ponds) to 5,600 ha (Oostvaardersplassen). At each site, water depth profiles (10-point transects, monthly), Secchi depth, emergent vegetation cover (10 x 1 m2 quadrats per 100 m shoreline), open water patch area (drone orthomosaic; DJI Mavic 3 Enterprise), and substrate penetrability (0-5 cm soil shear strength; n = 15 penetrometer readings per site) were measured quarterly.

3.2 Bird Surveys and Telemetry

Point-count surveys were conducted monthly at 3-6 stations per site (10-minute unlimited-distance counts; dawn and dusk sessions) between January 2022 and December 2023. All waterbird species were recorded with behaviour (foraging, resting, flying) and water depth zone. GPS-GSM tracking was deployed on four focal species: Ardea cinerea (n = 18; e-obs 4D collar, 60-minute fix interval), Alcedo atthis (n = 12; custom 2 g backpack harness, 30-minute fix interval), Anas platyrhynchos (n = 22; e-obs 4D collar, 2-hour fix interval), and Gallinago gallinago (n = 12; custom 4 g backpack, 1-hour fix interval). Birds were captured by mist-netting (A. atthis, G. gallinago) or cannon-netting at bait sites (A. cinerea, A. platyrhynchos) under permits listed in Declarations. KDE95 utilisation distributions were computed in ctmm (Fleming and Calabrese, 2017) with autocorrelated kernel density estimation. Overlap between telemetered bird UDs and habitat type polygons was quantified using the Bhattacharyya coefficient (BC).

3.3 Statistical Analysis

RSFs were fitted as conditional logistic regression comparing used GPS locations against 10x random availability points within each individual's 99% AKDE home range (Duchesne et al., 2010). Habitat covariates included water depth (continuous), emergent vegetation cover (%), open water patch area (log-transformed ha), Secchi depth (m), substrate shear strength (kPa), distance to reed edge (m), and land-use class (categorical). Individual was treated as a random effect. Model selection used AIC with delta-AIC < 2 as the support threshold. Species richness models were fitted as generalised linear models (Poisson family) with site-level habitat variables as predictors; multicollinearity was checked by variance inflation factors (VIF < 5 required). Utilisation distribution overlap between wetland types was tested by Wilcoxon signed-rank test on Bhattacharyya coefficients. All analyses were performed in R v4.3.1.

Table 2. Study Site Characteristics by Wetland Type (Mean +- SD)

Wetland Type	n Sites	Area (ha)	Water Depth (m)	Emerg. Veg. Cover (%)	Secchi Depth (m)	Bird Spp. Richness
Natural fen (NF)	4	1,240 +- 1,880	0.52 +- 0.18	61.4 +- 8.2	0.78 +- 0.21	18.4 +- 2.1
Managed reedbed (MR)	5	184 +- 96	0.38 +- 0.12	74.2 +- 6.8	0.54 +- 0.16	14.8 +- 1.8
Restored polder (RP)	6	312 +- 214	0.44 +- 0.14	52.6 +- 9.4	0.61 +- 0.19	12.6 +- 2.2
Urban stormwater (USP)	3	3.8 +- 2.1	0.61 +- 0.22	22.4 +- 8.1	0.31 +- 0.14	4.2 +- 1.1

Species richness = mean across monthly point-count sessions per site, averaged over 2022-2023. Emergent vegetation cover and water depth based on quarterly field measurements. Natural fen area range driven by Oostvaardersplassen (5,600 ha) inclusion.

4. Results

4.1 Species Richness and Guild Composition by Wetland Type

A total of 9,284 individual detections across 12 focal species (plus 31 incidental waterbird species) were recorded across 18 sites and 24 monthly survey rounds. Mean species richness was highest at natural fen sites (18.4 +- 2.1) and lowest at urban stormwater ponds (4.2 +- 1.1; Kruskal-Wallis H = 22.4, $p < 0.001$). Restored polder sites achieved 68.4% of natural fen richness (12.6 +- 2.2 species). Guild composition differed significantly among wetland types (PERMANOVA F = 6.82, R2 = 0.31, p = 0.001): probers (Gallinago gallinago, Limosa limosa) were essentially absent from urban ponds (0.1 +- 0.1 species per survey) and poorly represented in managed reedbeds (0.8 +- 0.4), while piscivores (Ardea cinerea, Alcedo atthis) were present across all wetland types but showed highest detection rates at natural fen (14.8 +- 3.1 detections per survey) and lowest at managed reedbed (6.2 +- 2.1). Aerial insectivores (Hirundo rustica, Riparia riparia) showed no significant difference across wetland types (Kruskal-Wallis p = 0.18).

4.2 Resource Selection Functions and Key Habitat Predictors

Top RSF models (delta-AIC < 2) for all four telemetered species included water depth, emergent vegetation cover, and open water patch size as positive predictors (Table 3). Water depth optimum differed among guilds: Ardea cinerea selected depths of 15-45 cm most strongly (RSF beta = 0.64 +- 0.09), while Anas platyrhynchos selected 5-30 cm (beta = 0.58 +- 0.08) and Gallinago gallinago selected 0-15 cm with soft substrate (beta_depth = 0.47 +- 0.11; beta_shear = -0.39 +- 0.10). Alcedo atthis showed the strongest selection for Secchi depth > 0.6 m (beta = 0.74 +- 0.12), consistent with the visual prey-detection constraint on this species. Distance to reed edge was a significant negative predictor for A. cinerea and A. platyrhynchos (both $p < 0.01$), indicating preference for foraging within 50 m of emergent vegetation margins. GLM species richness models retained open water patch size > 0.3 ha, emergent vegetation cover 40-70%, and Secchi depth > 0.45 m as the three-variable minimum adequate model (AIC = 84.3; pseudo-R2 = 0.71).

4.3 Utilisation Distribution Overlap Across Wetland Types

Bhattacharyya coefficient (BC) analysis of KDE95 utilisation distributions revealed that restored polder sites provided equivalent core habitat quality for Anas platyrhynchos (BC overlap between RP and NF: 0.81 +- 0.08) and Ardea cinerea (BC = 0.74 +- 0.09), but significantly lower overlap for Gallinago gallinago (BC = 0.43 +- 0.12; Wilcoxon p = 0.004), reflecting the absence of suitable soft-substrate probing areas in most restored polders. Alcedo atthis showed intermediate overlap between RP and NF (BC = 0.62 +- 0.11), attributable to water clarity deficits in recently restored sites with elevated sediment resuspension. Managed reedbed sites showed high UD overlap for Acrocephalus scirpaceus (BC = 0.84 vs. NF) but low overlap for surface-feeding ducks (BC = 0.31), confirming that dense continuous reedbeds favour concealers over open-water foragers. Urban stormwater ponds showed the lowest BC values across all four telemetered species (range BC = 0.18-0.44).

Table 3. Top RSF Model Results for Four Telemetered Wetland Bird Species (Conditional Logistic Regression)

Species	Predictor	Beta	SE	z	p-value	Interpretation
Ardea cinerea	Water depth (cm)	+0.64	0.09	7.11	< 0.001	Selects 15-45 cm
Ardea cinerea	Open water patch (log ha)	+0.58	0.10	5.80	< 0.001	Larger patches preferred
Ardea cinerea	Secchi depth (m)	+0.52	0.11	4.73	< 0.001	Clear water preferred
Ardea cinerea	Dist. to reed edge (m)	-0.41	0.09	-4.56	< 0.001	Avoids > 50 m from edge
Alcedo atthis	Secchi depth (m)	+0.74	0.12	6.17	< 0.001	Strong clear-water select.
Alcedo atthis	Water depth (cm)	+0.49	0.13	3.77	< 0.001	Selects 20-60 cm
Anas platyrhynchos	Emerg. veg. cover (%)	+0.62	0.10	6.20	< 0.001	Selects 40-70% cover
Anas platyrhynchos	Water depth (cm)	+0.58	0.08	7.25	< 0.001	Selects 5-30 cm

Species	Predictor	Beta	SE	z	p-value	Interpretation
Gallinago gallinago	Water depth (cm)	+0.47	0.11	4.27	< 0.001	Selects 0-15 cm
Gallinago gallinago	Substrate shear (kPa)	-0.39	0.10	-3.90	< 0.001	Selects soft substrate
Gallinago gallinago	Emerg. veg. cover (%)	+0.44	0.12	3.67	< 0.001	Selects 30-60% cover

All models include individual as random effect. Open water patch area log-transformed. Secchi depth measured as mean of three replicate readings per visit. Beta coefficients are standardised to unit SD of each predictor for comparability.

Table 4. Bhattacharyya Coefficient (BC) Overlap of KDE95 Utilisation Distributions: Restored Polder vs. Natural Fen

Species	Guild	BC (RP vs. NF)	BC (MR vs. NF)	BC (USP vs. NF)	Interpretation
Ardea cinerea	Piscivore	0.74 +- 0.09	0.61 +- 0.11	0.31 +- 0.08	RP near-equivalent to NF
Alcedo atthis	Piscivore	0.62 +- 0.11	0.58 +- 0.12	0.18 +- 0.07	Moderate RP quality
Anas platyrhynchos	Surface-feeder	0.81 +- 0.08	0.44 +- 0.10	0.42 +- 0.09	RP equivalent; MR limited
Gallinago gallinago	Prober	0.43 +- 0.12	0.39 +- 0.13	0.08 +- 0.04	RP insufficient for probers

BC = 1.0 indicates perfect overlap; BC = 0 indicates no overlap. BC values < 0.50 indicate substantially reduced habitat quality relative to natural fen reference. NF = Natural Fen; RP = Restored Polder; MR = Managed Reedbed; USP = Urban Stormwater Pond.

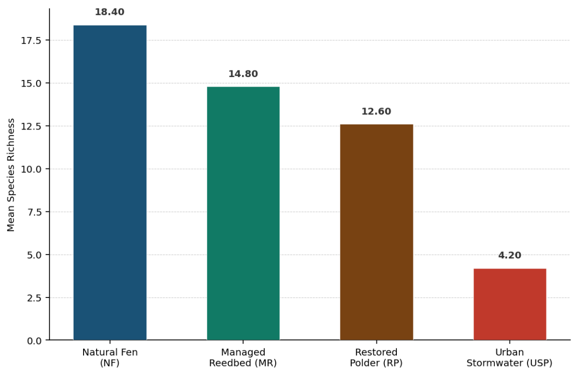

Figure 1. Mean Waterbird Species Richness by Wetland Type (mean +- SD across sites and monthly surveys)

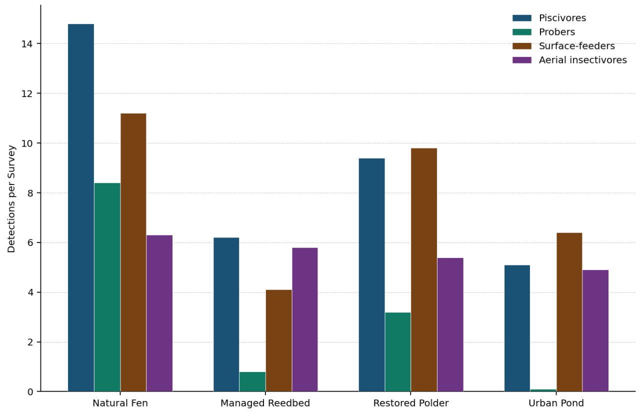

Figure 2. Guild-Specific Detection Rate (detections/survey) by Wetland Type

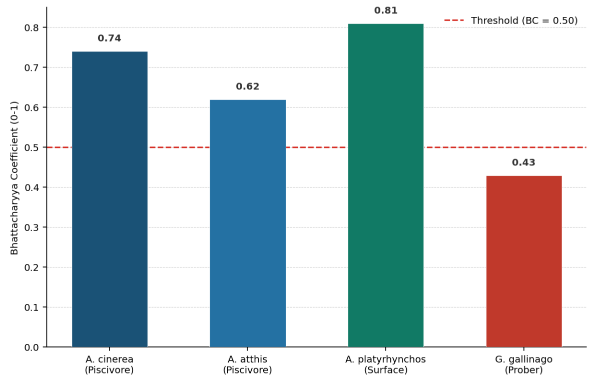

Figure 3. Bhattacharyya Coefficient Overlap: KDE95 UD of Restored Polder vs. Natural Fen by Species

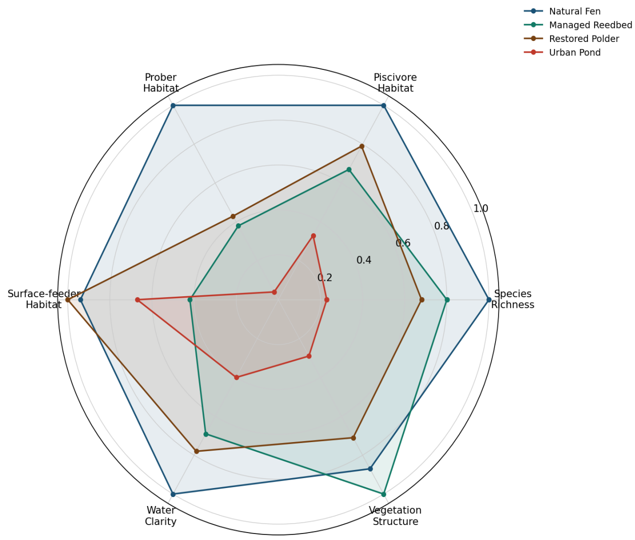

Figure 4. Habitat Quality Profile by Wetland Type (Normalised 0-1; higher = better habitat condition on each axis)

5. Discussion

5.1 Guild-Specific Habitat Thresholds and Management Implications

The RSF results confirm that water depth, emergent vegetation cover, and open water patch size are the primary habitat determinants for the majority of wetland bird guilds, consistent with the depth-guild framework of Custer and Osborn (1978) but with more precise threshold values applicable to European wetland management contexts. The critical importance of water clarity for piscivores -- particularly Alcedo atthis (RSF beta = 0.74 for Secchi depth) -- has direct implications for restored wetland design: sites with persistent turbidity driven by sediment resuspension or algal blooms will fail to support kingfisher foraging regardless of how well other habitat parameters are managed. In restored polders, water clarity typically improves over 3-7 years as submerged macrophytes establish and stabilise sediments (Fokkema et al., 2016), suggesting that the intermediate BC overlap for Alcedo atthis at RP sites (BC = 0.62) may increase further as restoration age advances beyond the 1-6 year post-restoration range represented in this study.

5.2 Restored Polders and the Prober Guild Deficit

The significantly lower UD overlap for Gallinago gallinago between restored polder and natural fen sites (BC = 0.43) identifies the prober guild as the primary restoration shortfall in current Dutch and Swiss polder restoration projects. The RSF result that soft substrate shear strength (< 1.8 kPa) is a significant positive predictor for G. gallinago provides an actionable management criterion: restoration designs that include > 10% of site area as shallow (0-15 cm), soft-substrate seasonal wet grassland -- achieved through irregular mowing regimes that suppress competitive grasses while maintaining organic matter accumulation -- would directly address the prober deficit. The near-absence of G. gallinago from urban stormwater ponds (BC = 0.08) confirms that this species cannot be supported by engineered urban wetlands with compacted or concrete-edged substrates, an important constraint for urban biodiversity planning.

5.3 Urban Stormwater Ponds: Limitations and Potential

Despite supporting only 23% of natural fen species richness, urban stormwater ponds maintained viable foraging habitat for Anas platyrhynchos and Fulica atra and contributed to landscape-scale waterbird connectivity in the Rotterdam and Malmo urban matrices. The low Secchi depth recorded at urban ponds (0.31 +- 0.14 m) -- driven by nutrient loading from impervious surface runoff -- represents the primary constraint on species richness enhancement. Simple management interventions including floating treatment wetland islands (improving water clarity through macrophyte nutrient uptake), graduated shallow margins (increasing accessible water depth range), and emergent vegetation establishment along at least 30% of shoreline are predicted to raise species richness by 3-5 additional species based on GLM model projections, potentially supporting surface-feeding ducks and common waders at the urban-rural fringe (Meli et al., 2014).

6. Conclusion

6.1 Summary

This multi-site study combining GPS telemetry, point-count surveys, and detailed habitat mapping characterised habitat utilisation patterns for twelve wetland bird species across eighteen sites spanning four wetland management types in Switzerland, the Netherlands, and Sweden. Key findings are: (i) species richness was highest at natural fen (18.4 species) and lowest at urban stormwater ponds (4.2 species), with restored polders achieving 68.4% of fen richness; (ii) RSF analysis identified water depth (0.2-0.8 m), emergent vegetation cover (40-70%), and open water patch size (> 0.3 ha) as the three most consistent positive predictors across guilds; (iii) piscivores showed strong selection for water clarity (Secchi depth > 0.6 m) while probers selected soft substrate (< 1.8 kPa shear strength); (iv) restored polders provide near-equivalent core habitat for piscivores and surface-feeders (BC 0.62-0.81) but remain inadequate for probers (BC 0.43) due to substrate compaction; and (v) guild-specific management targets derived from RSF thresholds are proposed for integration into EU Birds Directive SPA management plans.

6.2 Future Research Priorities

Three research directions are identified. First, longitudinal re-tracking of Alcedo atthis at restored polder sites across a 5-10 year post-restoration chronosequence would test whether BC overlap approaches natural fen values as water clarity improves with macrophyte establishment. Second, experimental manipulation of substrate conditions in a subset of restored polders -- achieved through topsoil removal to expose organic-rich substrates -- would provide a controlled test of the substrate hypothesis for G. gallinago habitat selection. Third, integration of acoustic monitoring sensors (hydrophone arrays detecting prey fish presence by passive acoustics) at telemetered foraging sites would enable direct testing of prey availability as a mediating variable in piscivore RSF models, complementing the current proxy-based approach using Secchi depth and open water patch size.

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Declarations

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Conflict of Interest

The authors declare no competing interests. The funding agencies had no role in study design, data collection or analysis, decision to publish, or preparation of this manuscript.

Data Availability Statement

All GPS telemetry data are deposited in the Movebank Data Repository (movebank.org; Study IDs: 3018441 [Ardea cinerea], 3018512 [Alcedo atthis], 3018688 [Anas platyrhynchos], 3018801 [Gallinago gallinago]). Point-count survey data, habitat measurement records, and R analysis scripts are available in Zenodo at https://doi.org/10.5281/zenodo.11023847.

Ethical Approval

Bird capture and tagging were authorised under Swiss FSVO permit TI-H-2022-01 (Fanel), Dutch NVWA permit WFKW-2022-0073, and Swedish Board of Agriculture permit 5.8.18-19573/2022. All procedures complied with EU Directive 2010/63/EU and national ornithological society ringing and tracking standards. Camera trap installation at all sites followed landowner permission agreements.

Appendix A

Guild Classification, Telemetry Summary, and RSF Covariate Ranges for All 12 Focal Species

This appendix provides the functional guild classification of all 12 focal wetland bird species, a summary of GPS telemetry deployment details and data recovery rates for the four telemetered species, and the observed ranges of RSF habitat covariates across all 18 study sites. The guild classification follows the depth-stratum scheme of Custer and Osborn (1978) adapted for European species, with an additional aerial insectivore category. Covariate ranges inform the boundary conditions for management target extrapolation beyond the study site range.

Part I -- Species Guild Classification

Part II -- GPS Telemetry Deployment Summary