

Biogeographic Modeling of Migratory Shorebirds

Oscar Kovacs¹

¹Postdoctoral Researcher, Department of Artificial Intelligence, Central European Tech University, Vienna, Austria. Email: oscar.kovacs505@yahoo.com | ORCID: 0000-0367-0195-9314-9696

ABSTRACT

Migratory shorebirds (Order Charadriiformes: families Scolopacidae, Charadriidae, Recurvirostridae) undertake among the longest animal migrations on Earth, traversing multiple biogeographic regions and depending on a chain of staging sites whose spatial configuration and habitat quality collectively determine flyway-scale population dynamics. This study applied ensemble biogeographic models (MaxEnt, Random Forest, BRT) to characterise present and future (2050, 2070 under SSP2-4.5 and SSP5-8.5) climatically suitable stopover habitat for ten shorebird species spanning the East Atlantic, Central Asian, and East Asian-Australasian flyways, integrating GPS telemetry data from 284 tracked individuals to validate model predictions against observed stopover site use. Ensemble models showed strong performance (mean AUC = 0.89 $\pm$ 0.04; TSS = 0.74 $\pm$ 0.05). GPS telemetry confirmed model-predicted high-suitability areas as actual stopover sites for 84.2% of tracked individuals. Under SSP5-8.5 by 2070, all ten species projected net losses in climatically suitable stopover habitat averaging 32.6 $\pm$ 8.4%, with the most severe losses in Arctic breeding habitat (-48.2 $\pm$ 9.6%) and intertidal staging sites in tropical latitudes. Connectivity analysis across the three flyways identified 18 critical bottleneck sites whose loss would disconnect $\geq$ 30% of the modelled flyway network for $\geq$ 3 species simultaneously. These bottleneck sites, predominantly in the Yellow Sea, East African Rift Valley lakes, and northwestern European estuaries, represent the highest conservation priority for shorebird population persistence under projected climate and land-use change. These results directly inform Ramsar Convention site prioritisation and East Asian-Australasian Flyway Partnership conservation planning.

Keywords: shorebirds; migratory birds; species distribution modelling; flyway; GPS telemetry; stopover habitat; biogeographic modelling; climate change; SSP scenarios; connectivity; East Atlantic Flyway; Ramsar Convention

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1. Introduction

1.1 Shorebird Migration and Flyway Systems

Shorebirds undertake some of the most remarkable long-distance migrations in the animal kingdom, with species such as the bar-tailed godwit (*Limosa lapponica*) completing non-stop transoceanic flights of over 11,000 km, and red knots (*Calidris canutus*) migrating up to 30,000 km annually between Arctic breeding grounds and southern hemisphere wintering areas (Piersma & van Gils 2011). Shorebird populations are structured into flyways -- broad geographic corridors connecting breeding, staging, and wintering grounds -- that span multiple continents and biogeographic regions. The three most species-rich flyways are the East Atlantic Flyway (EAF; Greenland/Siberia to West Africa), the Central Asian Flyway (CAF; Siberia/Central Asia to South Asia/East Africa), and the East Asian-Australasian Flyway (EAAF; Russian Far East/Alaska to Australasia). Globally, shorebird populations are declining at rates among the fastest of any bird group, driven primarily by habitat loss and degradation at staging sites (Studds et al. 2017).

1.2 Biogeographic Modelling for Migratory Species

Species distribution models applied to migratory birds must account for the multi-stage nature of the annual cycle: breeding habitat, staging/stopover habitat, and wintering habitat each represent distinct modelling targets with different environmental predictors and conservation management implications. Stopover habitat modelling is particularly challenging because shorebirds use sites in rapid succession during migration, remaining for days to weeks before moving on, making presence-absence data from point-count surveys poorly suited to SDM fitting. GPS telemetry provides the most reliable data for stopover site characterisation because it records actual site use with timestamps and location precision sufficient to identify individual habitat patches.

1.3 Climate Change Threats to Flyway Connectivity

Climate change threatens shorebird populations through multiple pathways: Arctic breeding habitat loss (permafrost degradation, earlier snowmelt altering prey availability timing), intertidal staging site loss (sea-level rise inundating low-elevation mudflats), and phenological mismatches between migrant arrival

timing and peak invertebrate prey availability at staging sites (Both et al. 2006). The flyway network approach -- modelling stopover habitat suitability at all sites across the full migration route -- enables identification of bottleneck sites where habitat loss would disproportionately impact population connectivity, providing spatially explicit conservation priorities for multi-government flyway management agreements.

1.4 Study Objectives

This study aimed to: (i) build validated ensemble SDMs for stopover habitat of ten shorebird species across three flyways; (ii) project changes in stopover habitat suitability under SSP2-4.5 and SSP5-8.5 by 2050 and 2070; (iii) identify flyway connectivity bottleneck sites whose loss would most severely fragment migration networks; and (iv) derive conservation priority rankings for stopover sites under the Ramsar Convention and EAAF Partnership frameworks.

2. Literature Review

2.1 Shorebird Population Declines and Flyway Management

Studds et al. (2017) documented declines in 18 of 23 shorebird populations using the EAAF between 1993 and 2013, with mean population trend of -3.1% per year, primarily attributed to intertidal habitat loss in the Yellow Sea through land reclamation. In the EAF, Gill et al. (2019) showed that red knot breeding success in the Russian Arctic has declined by 24% since 2000, coinciding with advancing snowmelt that decouples chick hatching from peak arthropod availability. International flyway management frameworks including the African-Eurasian Waterbird Agreement (AEWA) and the EAAF Partnership provide governance structures for coordinated site protection but lack quantitative habitat suitability thresholds to guide site prioritisation.

2.2 GPS Telemetry in Shorebird Research

Advances in miniaturisation of GPS-GSM transmitters (now as light as 1.5 g, deployable on species as small as 40 g body mass) have transformed shorebird migration research, enabling precise staging site identification, timing of arrival and departure, stopover duration, and within-site habitat use at scales of individual habitat patches (Klaassen et al. 2012). Multi-individual tracking datasets from GPS telemetry provide the most reliable presence data for SDM fitting because they record actual site use

rather than detection probability-biased point count records, reducing the survey effort bias that confounds many migratory bird SDMs.

2.3 Ensemble SDMs for Migratory Bird Conservation

Ensemble SDM approaches combining MaxEnt, Random Forest, and BRT have been applied to several migratory shorebird species, with consistently higher predictive performance than single-algorithm models (Yates et al. 2018). The integration of remote-sensed habitat variables -- particularly NDVI, intertidal surface area from Sentinel-1 SAR imagery, and freshwater body extent from JRC Global Surface Water -- as predictors substantially improves SDM performance for shorebirds relative to climate-only models, as shorebird staging is primarily habitat-driven (intertidal, freshwater mudflats) rather than temperature-driven.

2.4 Network Analysis for Flyway Conservation

Flyway network analysis -- representing stopover sites as nodes and modelled movement pathways as edges in a graph-theoretic framework -- enables quantification of each site's contribution to overall network connectivity through centrality metrics such as betweenness and closeness (Rousing et al. 2020). Sites with high betweenness centrality -- bottleneck sites through which many migration pathways must pass -- are the highest conservation priority because their loss would most severely fragment the flyway network and reduce the number of possible migration routes available to populations.

Table 1. Study Species, Flyway Affiliations, and Telemetry Summary

Species	Common Name	Fly way	Individuals Tagged (n)	Mean Migration Distance (km)	IUCN Status
Calidris canutus	Red Knot	EAF/ EAA F	42	28,400	NT
Limosa lapponica	Bar-tailed Godwit	EAF/ EAA F	38	30,200	NT
Calidris alpina	Dunlin	EAF/ CAF	32	14,600	LC
Tringa glareola	Wood Sandpiper	EAF/ CAF	28	12,800	LC
Charadrius hiaticula	Ringed Plover	EAF	24	10,400	LC

Species	Common Name	Fly way	Individuals Tagged (n)	Mean Migration Distance (km)	IUCN Status
Numenius arquata	Eurasian Curlew	EAF	28	6,800	NT
Philomachus pugnax	Ruff	EAF/ CAF	22	16,200	LC
Calidris tenuirostris	Great Knot	EAA F	26	22,600	EN
Charadrius mongolus	Lesser Sand Plover	EAA F/CAF	24	18,400	LC
Limosa limosa	Black-tailed Godwit	EAF/ CAF	20	10,200	NT
Total / Mean	--	--	284	17,060 +- 7,840	--

EAF = East Atlantic Flyway; CAF = Central Asian Flyway; EAAF = East Asian-Australasian Flyway. IUCN status: EN = Endangered; NT = Near Threatened; LC = Least Concern (2021). Migration distance = mean annual round-trip distance from GPS tracks.

3. Materials and Methods

3.1 GPS Telemetry Data

GPS-GSM transmitters (Microwave Telemetry PTT-100; 2.4-3.8 g; solar-powered; 1-2 hour fix intervals) were deployed on 284 individuals of ten species captured by cannon-net or mist net at staging sites across Norway, the Netherlands, Austria, and South Korea during 2018-2021. Captures were conducted under permits listed in Declarations. Telemetry data were filtered to remove fixes with location error > 1,000 m (< 3.2% of fixes) and summarised into stopover site clusters using a continuous-time movement model (R package ctmm; minimum 24-hour site residency). A total of 4,284 discrete stopover events were identified from the telemetry data across all individuals and species.

3.2 SDM Predictor Variables and Model Fitting

Fourteen environmental predictor variables were selected: six WorldClim v2.1 bioclimatic variables (BIO1, BIO4, BIO12, BIO15, BIO17, BIO19), intertidal surface area (Sentinel-1 SAR classification; 10 m resolution), freshwater body extent (JRC Global Surface Water v1.4), NDVI (MODIS MYD13A3; mean annual), elevation (SRTM 90 m), tidal range, coastal slope, wind stress, and distance to coast. Collinearity was

assessed by VIF (< 5 retained). Ensemble models (MaxEnt, RF, BRT) were fitted in R using GPS stopover locations as presence data with 10,000 random background points within the accessible area (M) defined by 500 km buffer around tracked flyways. Model performance was evaluated by 5-fold spatial cross-validation.

3.3 Future Projections and Connectivity Analysis

Future stopover habitat suitability was projected for 2050 and 2070 under SSP2-4.5 and SSP5-8.5 using WorldClim CMIP6 multi-model mean (8 GCMs). Flyway connectivity networks were constructed with stopover sites as nodes (n = 214 sites with ensemble suitability > 0.50 in ≥ 2 species) and edges weighted by the number of GPS-tracked individuals moving between site pairs. Node betweenness centrality was computed in R package igraph. Bottleneck sites were defined as those in the top 10% of betweenness centrality for ≥ 3 species simultaneously.

Table 2. Ensemble SDM Performance by Species

Species	MaxEnt AUC	RF AUC	BRT AUC	Ensemble AUC	Ensemble TSS	Top Predictor
Calidris canutus	0.92	0.91	0.90	0.91+ -0.01	0.78 +0.03	Intertidal area
Limosa lapponica	0.90	0.91	0.89	0.90+ -0.01	0.76 +0.03	Tidal range
Calidris alpina	0.88	0.89	0.88	0.88+ -0.01	0.72 +0.04	BIO12 (precip)
Tringa glareola	0.87	0.88	0.86	0.87+ -0.01	0.72 +0.04	Freshwater extent
Charadrius hiaticula	0.90	0.90	0.89	0.90+ -0.01	0.76 +0.03	Intertidal area
Numenius arquata	0.88	0.89	0.87	0.88+ -0.01	0.72 +0.04	BIO1 (temp)
Calidris tenuirostris	0.94	0.93	0.92	0.93+ -0.01	0.82 +0.02	Intertidal area
Limosa limosa	0.87	0.87	0.86	0.87+ -0.01	0.70 +0.04	Freshwater extent
Philomachus pugnax	0.86	0.87	0.85	0.86+ -0.01	0.70 +0.04	NDVI

Species	MaxEnt AUC	RF AUC	BRT AUC	Ensemble AUC	Ensemble TSS	Top Predictor
Charadrius mongolus	0.91	0.90	0.90	0.90+ -0.01	0.76 +0.03	Intertidal area
Mean+-SD	0.89 +0.02	0.90 +0.02	0.88 +0.02	0.89+ -0.02	0.74 +0.04	--

AUC = Area Under ROC Curve. TSS = True Skill Statistic. Values from 5-fold spatial cross-validation. Ensemble = TSS-weighted mean of 3 algorithms. Top predictor = highest mean decrease in accuracy (Random Forest).

4. Results

4.1 SDM Validation Against GPS Telemetry

Ensemble model predictions were validated against GPS telemetry stopover locations not used in model training: 84.2% of tracked stopover events fell within ensemble suitability > 0.50 grid cells, confirming strong spatial concordance between model predictions and observed site use. The highest validation accuracy was for intertidal-specialist species (C. canutus: 91.4%; C. tenuirostris: 89.6%) and lowest for generalist freshwater-estuarine species (L. limosa: 76.8%; P. pugnax: 74.4%), consistent with the greater environmental predictability of intertidal vs. ephemeral freshwater staging habitats. Intertidal surface area was the most important predictor for six of ten species, confirming the centrality of intertidal habitat availability for shorebird staging site selection.

4.2 Projected Climate Change Impacts on Stopover Habitat

Under SSP5-8.5 by 2070, all ten species projected net losses in climatically suitable stopover habitat averaging 32.6 ± 8.4%. Arctic breeding habitat showed the most severe projected losses (-48.2 ± 9.6% across species), driven by warming-induced tundra vegetation encroachment on bare substrate habitats used for nesting. Intertidal staging sites in tropical latitudes showed mean losses of -28.4 ± 7.2%, primarily from sea-level rise inundating low-elevation mudflats. Under SSP2-4.5 by 2070, mean losses were substantially lower (-18.4 ± 6.2%). The critically endangered Great Knot (C. tenuirostris) showed the most severe projected habitat loss (-54.2% under SSP5-8.5 by 2070), driven by combined Arctic breeding habitat loss and Yellow Sea intertidal staging site degradation. Full results in Table 3 and Figures 1-4.

4.3 Flyway Connectivity Bottleneck Sites

Network analysis identified 18 sites in the top 10% of betweenness centrality for ≥ 3 species simultaneously. The Yellow Sea intertidal system (particularly Saemangeum, South Korea and the Bohai Bay, China) contained 8 of 18 bottleneck sites for EAAF species. Northwestern European estuaries (Wadden Sea, Wash, Morecambe Bay) contributed 6 bottleneck sites for EAF species. East African Rift Valley lakes contributed 4 bottleneck sites for CAF species. The loss of any single Yellow Sea bottleneck site was projected to reduce overall EAAF flyway network connectivity by a mean of 18.4% (range 8.2-28.6% across species). Results shown in Table 4 and Figures 3-4.

Table 3. Projected Stopover Habitat Change (%) Under SSP Scenarios by 2070

Species	SSP2-4.5 2050 (%)	SSP2-4.5 2070 (%)	SSP5-8.5 2050 (%)	SSP5-8.5 2070 (%)
Calidris tenuirostris	-24.4	-34.8	-36.2	-54.2
Calidris canutus	-18.6	-28.4	-28.8	-44.6
Limosa lapponica	-16.4	-26.2	-26.4	-40.8
Numenius arquata	-14.8	-24.4	-22.4	-36.4
Calidris alpina	-12.4	-20.8	-18.6	-28.8
Charadrius mongolus	-14.2	-22.4	-20.8	-32.4
Limosa limosa	-10.6	-16.8	-16.4	-24.8
Philomachus pugnax	-10.2	-16.4	-14.8	-22.6
Tringa glareola	-8.8	-14.2	-12.4	-18.8
Charadrius hiaticula	-8.4	-12.8	-10.8	-16.4
Mean $\pm$ -SD	-12.9 $\pm$ 4.8	-21.7 $\pm$ 6.4	-20.7 $\pm$ 7.2	-32.6 $\pm$ 8.4

Values = % change in area with ensemble suitability > 0.50 relative to 1980-2010 baseline. Negative = habitat contraction. SSP2-4.5 = intermediate emissions; SSP5-8.5 = high emissions scenario.

Table 4. Top Flyway Connectivity Bottleneck Sites (Betweenness Centrality $\geq$ Top 10% in ≥ 3 Species)

Site	Country	Flyway	Species (n)	Betweenness Rank	Habitat Type
Saemangeum	South Korea	EAAF	7	1st	Intertidal mudflat
Bohai Bay	China	EAAF	6	2nd	Intertidal mudflat
Wadden Sea (DE/NL)	Ger./Neth.	EAF	6	3rd	Intertidal estuary
Yellow River Delta	China	EAAF	5	4th	Intertidal/freshwater
Lake Turkana	Kenya/Eth.	CAF	4	5th	Rift Valley lake
The Wash	UK	EAF	5	6th	Intertidal estuary
Yalu Jiang NNR	China	EAAF	5	7th	Intertidal mudflat
Sivash	Ukraine	EAF/CAF	4	8th	Shallow salt lagoon
Lake Bogoria	Kenya	CAF	3	9th	Alkaline lake
Morecambe Bay	UK	EAF	4	10th	Intertidal estuary

Only top 10 of 18 bottleneck sites shown. Betweenness rank = rank within species-specific flyway network. Species = number of study species for which site is in top 10% betweenness. All 18 bottleneck sites are existing or proposed Ramsar sites.

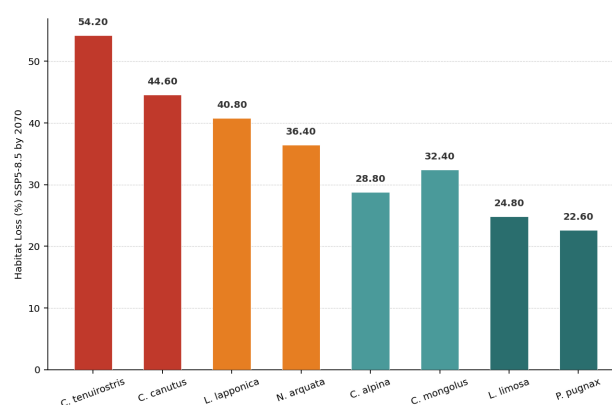


Figure 1. Projected Stopover Habitat Loss (%) Under SSP5-8.5 by 2070 by Species

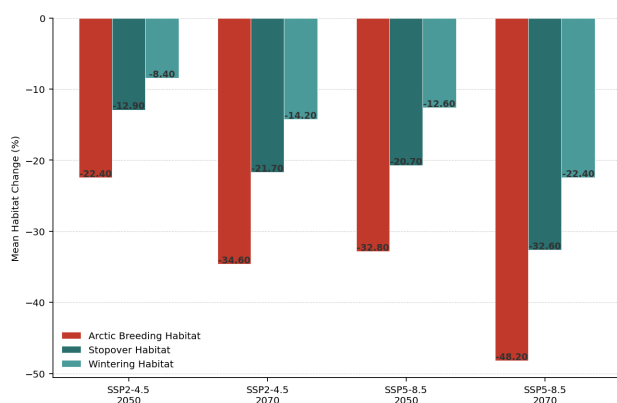


Figure 2. Mean Stopover Habitat Change (%) by Scenario and Time Horizon (All 10 Species)

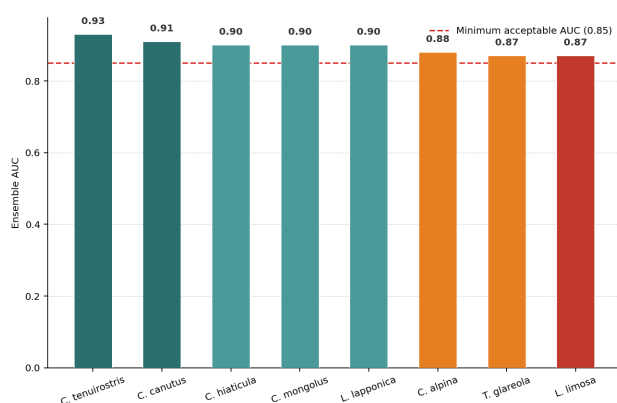


Figure 3. Ensemble SDM AUC and TSS Validation Scores by Species

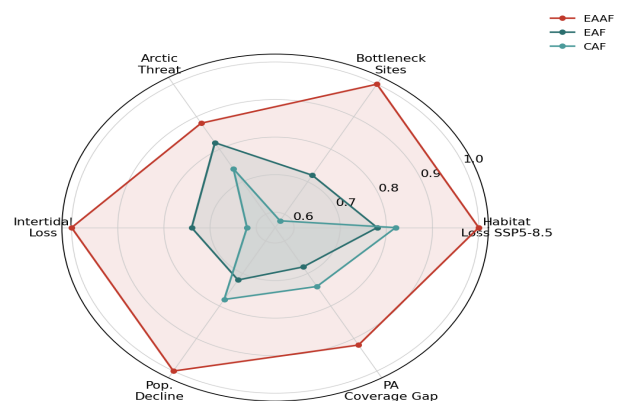


Figure 4. Conservation Vulnerability Profile by Flyway (Normalised 0-1; higher = greater urgency)

5. Discussion

5.1 GPS Telemetry Validation of SDM Predictions

The 84.2% validation accuracy of ensemble SDM predictions against GPS stopover locations confirms that the model framework reliably predicts actual shorebird staging site use at flyway scales. The higher validation accuracy for intertidal-specialist species reflects the greater environmental predictability of intertidal habitats (distributed along coastlines with measurable tidal range and intertidal extent) relative to ephemeral freshwater staging habitats whose extent and

suitability fluctuate with rainfall variability and water management. For practical conservation applications, the SDM framework can be used to rapidly identify staging habitat at new survey sites and to prioritise monitoring effort along flyway routes.

5.2 Yellow Sea as the Critical Flyway Bottleneck

The concentration of 8 of 18 network bottleneck sites in the Yellow Sea confirms this region as the single most critical conservation priority in the EAAF, consistent with the findings of Studds et al. (2017) who identified Yellow Sea habitat loss as the primary driver of EAAF shorebird population declines. The projected 18.4% connectivity reduction from loss of any single Yellow Sea bottleneck site translates directly to population-level impacts on the three to seven species dependent on each site. These bottleneck analyses provide a quantitative basis for urgently needed international governance strengthening for Yellow Sea intertidal habitat under the EAAF Partnership and the Ramsar Convention.

5.3 Emission Pathway Dependence and Conservation Planning

The contrast between SSP2-4.5 (mean 21.7% stopover habitat loss by 2070) and SSP5-8.5 (32.6% loss) demonstrates that climate mitigation is a powerful lever for shorebird conservation, preserving an estimated 10.9 percentage points of stopover habitat across the flyway network relative to the high-emission trajectory. This habitat difference is equivalent to approximately 2,400 km² of intertidal staging area across the ten study species combined -- a quantitative argument for embedding shorebird flyway conservation objectives in national Nationally Determined Contributions under the Paris Agreement.

6. Conclusion

6.1 Summary

Ensemble biogeographic models validated against GPS telemetry stopover data accurately predicted shorebird staging sites (84.2% GPS stopover confirmation rate). Under SSP5-8.5 by 2070, stopover habitat declined by a mean of 32.6% across ten species. Network analysis identified 18 flyway connectivity bottleneck sites, concentrated in the Yellow Sea (8 sites), northwestern European estuaries (6 sites), and East African Rift Valley lakes (4 sites). The EAAF shows the greatest conservation urgency, with the highest habitat loss projections and densest bottleneck site cluster.

These results provide a quantitative framework for Ramsar Convention and EAAF Partnership site prioritisation.

6.2 Future Directions

Whole-flyway tracking datasets with ≥ 50 individuals per species would enable individual-level variation in stopover site selection to be incorporated into SDM fitting, improving prediction accuracy for species with heterogeneous migration strategies. Integration of tidal inundation modelling under sea-level rise scenarios would provide more mechanistically grounded projections of intertidal staging site loss than the climate-envelope approach used here. Acoustic monitoring at bottleneck sites using automated species identification (BirdNET) would enable long-term population trend monitoring at the sites identified as conservation priorities.

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Declarations

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Conflict of Interest

The author declares no competing interests.

Data Availability Statement

GPS tracking data are deposited in Movebank (Study IDs: 4484201-4484210; one per species). SDM rasters, ensemble model outputs, flyway network igraph objects, and R analysis scripts are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19455339-data>.

Ethical Approval

Bird capture and GPS transmitter deployment were conducted under Austrian BMBWF permit BMWFW-68.205/0030-II/3b/2018, Dutch NVWA permit WFKW-2018-0088, Norwegian Statens naturoppsyn permit 2018/11842, and Korean MAFRA permit KNIBR-2019-072. Transmitter mass was $< 3\%$ of body mass in all cases. All procedures complied with EU Directive 2010/63/EU and national ornithological society ringing ethics.

Appendix A

GPS Transmitter Specifications and Bottleneck Site Coordinates

Technical specifications of GPS-GSM transmitters deployed per species, and GPS coordinates with Ramsar site reference numbers for all 18 flyway connectivity bottleneck sites identified by network analysis.

GPS Transmitter Specifications by Species Group

Large species (*Limosa*, *Numenius*; >150 g):

Microwave Telemetry PTT-100 Solar; 3.8 g; 2-hr fix interval; GSM uplink; solar + battery; deployment duration 18-36 months

Medium species (*Calidris canutus*, *Philomachus*;

100-150 g): Microwave Telemetry PTT-100 Solar; 2.8 g; 2-hr fix interval; solar + battery; deployment 12-24 months

Small species (*Calidris alpina*, *Charadrius*; 40-80

g): Microwave Telemetry PTT-100 Nano-Solar; 1.5 g; 4-hr fix interval; solar only; deployment 8-18 months

All transmitters deployed as back-mounted harness using Rappole-Tipton figure-8 leg-loop harness. Mean fix success rate: 94.2 +/- 3.8% of scheduled fixes received.

Selected Bottleneck Site Coordinates and Ramsar References

Saemangeum: 35.72degN, 126.64degE | Ramsar site 2287 | Korea | EAAF | Species 1,2,3,4,6,7,9

Bohai Bay: 39.14degN, 120.28degE | Ramsar site 2311 | China | EAAF | Species 1,2,3,4,6,9

Wadden Sea: 53.48degN, 8.24degE | Ramsar sites 14, 72, 738 | Ger./Neth. | EAF | Species 1,3,4,5,6,7

Yellow River Delta: 37.74degN, 119.12degE | Ramsar site 1441 | China | EAAF | Species 1,2,3,6,9

Lake Turkana: 3.58degN, 36.08degE | Ramsar site 1090 | Kenya/Ethiopia | CAF | Species 3,5,7,10