Site-level connectivity identified from multiple sources of movement data to inform conservation of a migratory bird

Martin Beal[1*], Josh Nightingale[2], João R. Belo[3,4], Chris Batey[5], Heinrich Belting[6], Pierrick Bocher[7,] Malcolm Burgess[5], Taylor B. Craft [4,8,9], Nicola Crockford[5], Philippe Delaporte[10], Lynda Donaldson[11,5], Guillaume Gélinaud[12], Jennifer A. Gill[13], Tómas G. Gunnarsson[2], Böðvar Þórisson[2], Jorge S. Gutiérrez[14], Jos C.E.W. Hooijmeijer[4,8], Ruth A. Howison[9,4], Philip Hunke[15], Loïc Jomat[10], Hilger Lemke[16], Jürgen Ludwig[16], Frank A. Majoor[17], Christopher Marlow[6,18], José A. Masero[14], Johannes Melter[19], Ian Nicholson[20], Manuel Parejo[21], Barry O'Mahony[22], Esko Pasanen[22], Jorma Pessa[23], Theunis Piersma [4,8,24], Afonso D. Rocha[14,3], Frederic Robin[9,10], Maja Roodbergen[17], Pierre Rousseau[10] Volker Salewski[15], Luis Schmidt[15], Jennifer Smart[5], Anna Staneva[25], T. Lee Tibbitts[26], Sami Timonen[27], José A. Alves[3,2] & Maria P. Dias[1]

Institutions:

1. cE3c - Centre for Ecology, Evolution and Environmental Changes & CHANGE - Global Change and Sustainability Institute, Department of Animal Biology, Faculty of Sciences of the University of Lisbon, Campo Grande, 1749-016 Lisboa, Portugal
2. South Iceland Research Centre, University of Iceland, Laugarvatn, Iceland
3. Department of Biology & CESAM, Centre for Environmental and Marine Studies, University of Aveiro, Aveiro, Portugal
4. BirdEyes, Centre for Global Ecological Change at the Faculties of Science & Engineering and Campus Fryslân, University of Groningen, Zaailand 110, 8911 BN Leeuwarden, The Netherlands
5. RSPB Centre for Conservation Science, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK
6. NLWKN - Niedersächsischer Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz, Naturschutzstation Dümmer, Am Ochsenmoor 52, 49448 Hüde, Germany

7. Laboratory Littoral Environnement et Societés (LIENSs), UMR 7266 La Rochelle University- CNRS, France
8. Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences, University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands
9. Knowledge Infrastructures Department, Campus Fryslân, University of Groningen, Groningen, Netherlands
10. Ligue pour la Protection des Oiseaux (LPO), Réserve Naturelle de Moëze-Oléron, Saint-Froult, France
11. WWT, Slimbridge, Gloucestershire, GL2 7BT, UK
12. Bretagne Vivante, Réserve Naturelle des marais de Séné, Route de Brouel, 56860 Séné, France
13. School of Biological Sciences, University of East Anglia, Norwich Research Park, Norwich, NR7 4TJ, UK
14. Ecology in the Anthropocene, Associated Unit CSIC-UEX, Faculty of Sciences, University of Extremadura, 06006 Badajoz, Spain
15. Michael-Otto-Institut im NABU, Goosstroot 1, 24861 Bergenhusen, Germany
16. NLWKN - Niedersächsischer Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz, Naturschutzstation Unterelbe, Alte Hafenstraße 2, D-21729 Freiburg/Elbe, Germany
17. Sovon Dutch Centre for Field Ornithology, Nijmegen, The Netherlands
18. NLWKN - Niedersächsischer Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz, Naturschutzstation Unterelbe, Im Dreieck 12, D-26127 Oldenburg
19. Bio-Consult GbR, Dulings Breite 6-10, 49191 Belm, Germany
20. Humber Wader Ringing Group, York, UK
21. Conservation Biology Research Group, Department of Anatomy, Cell Biology and Zoology, Faculty of Sciences, University of Extremadura
22. Independent researcher
23. Center for Economic development, Transport and the Environment, North Ostrobothnia, P.O.Box 86, FIN-90101 Oulu, Finland
24. Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, PO Box 59, 1790 AB Den Burg, Texel, The Netherlands
25. BirdLife International, The David Attenborough Building, CB2 3QZ, Cambridge, United Kingdom
26. U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, Alaska, 99508 USA

27. Center for Economic development, Transport and the Environment, North Ostrobothnia, Veteraanikatu 1, P.O. Box 86, FIN-90101 Oulu, Finland

*Corresponding author

†Present address

Abstract

1. Migratory birds depend on a suite of sites across their annual cycles, making them vulnerable to a wide variety of anthropogenic pressures. Current area-based conservation measures have been found inadequate to safeguard migratory birds, in part due to a lack of consideration for the connectivity between sites mediated by the movements of individuals.

2. To address this issue, we develop a network analysis integrating different types of individual movement data for a migratory shorebird, the Black-tailed Godwit (*Limosa limosa)*, across the East Atlantic Flyway. Leveraging metal-ring recoveries, colour-ring re-sightings, and satellite tracking from over 10,000 individual godwits, we quantify variation in connectivity between sites across the migratory range, using two weighted metrics to address sampling biases.

3. Colour-ring re-sightings provided the largest number of sites (70%) and links (60% for November–May, and 43% for June–October) overall, followed by tracking data (50% of sites, 49% and 63% of links per season) and ring recoveries (25% of sites, <1% of links per season), with clear regional variation in datatype contributions. Sampling completeness of the network structure varied with longitude, with information particularly lacking in central-eastern countries of both Europe and Africa.

4. We identified 49 sites playing a disproportionate role in the site network, each with direct connections to 48 (interquartile range 32-84) other sites, on average. Just 23 (47%) top sites are formally recognized for their international importance for Black-tailed Godwits and 33 (67%) were robust to sampling incompleteness. Across all 1058 sites, 20% lacked protected area coverage, and per site, 44% (44% +/- SD) of bird relocations fell within protected areas.

5. Integrating multiple sources of data improved geographical coverage and completeness of the site network, allowing us to quantify the importance of sites in terms of connectivity across the flyway. Our results highlight shortcomings of existing area-based conservation measures and add value to ongoing efforts to identify important sites for migratory birds.
6. *Policy implications:* The increasing availability of individual movement data provides valuable opportunities to reveal the inter-dependence of sites used by migratory species, which can help identify priority areas and facilitate flyway-scale management.

Keywords

Area-based conservation, animal migration, bird ringing, movement ecology, network analysis, protected areas, satellite tracking, shorebirds

Introduction

Migratory birds move between disjunct habitats to meet seasonal demands, connecting numerous places. This dependence on multiple locations complicates the effective conservation of migratory birds, as the various locations used across the year often fall under varying legal frameworks and management regimes (DeLuca et al., 2023; Martin et al., 2007). The first UN report on the State of the World’s Migratory Species describes a dire situation (UNEP-WCMC, 2024), with population declines in 44% of migratory species due to unmitigated threats occurring in some parts of their ranges (Bairlein, 2016; Erickson et al., 2018).

Area-based conservation measures (e.g., protected areas) are one of the main tools for maintaining and restoring biodiversity (Le Saout et al., 2013). Global coverage of protected areas is, however, insufficient for conserving populations of migratory birds (Runge et al., 2015). For protected area networks to be effective for migratory species, there must be explicit consideration made for the functional linkages existing between sites used at different times of the year (DeLuca et al., 2023; Erickson et al., 2018). Important sites for biodiversity, such as the Ramsar Convention's Wetlands of International Importance or Important Bird and Biodiversity Areas (IBAs), are often used to inform protected area designation (Donald et al., 2019). These frameworks use either qualitative or quantitative criteria to assess the site's contribution to the persistence of a species or ecosystem (IUCN, 2016). Most site-based conservation frameworks consider only the standalone importance of a site, e.g., number of individuals found there (Donald et al., 2019). Assessing sites in isolation, however, ignores the role of a given area within the network of sites used by a mobile population (Navedo and Piersma, 2023; Nightingale et al., 2023; Xu et al., 2022).

During migration, individuals visit specific sites for breeding, refuelling, moulting, or over-wintering (Alerstam, 1993), forming a web of connections often referred to as the 'migratory site network' (Xu et al., 2022). The importance of maintaining connectivity between sites across the annual cycle for migratory species has long been recognized (Sutherland, 1997). However, despite most nations committing to deliver 'ecological connectivity' (the 'connection of habitats without hindrance'; UNEP-CMS, 2024), under multilateral environmental agreements like the Convention on Migratory Species, formal mechanisms for identifying important sites in terms of connectivity are lacking (Xu et al., 2022). To begin filling this gap, tools are urgently needed for characterizing site-level connectivity across the annual cycle of migratory species.

Network analysis, a graph-theoretical approach for representing complex systems of interactions, provides a useful framework for quantifying site connectivity (Jacoby and Freeman, 2016). In this context, a migratory site network is composed of sites (or 'nodes') connected via links (or 'edges') formed by the movements of individuals. A series of 'centrality' metrics can be derived to quantify the contribution of each site to the network structure (Rayfield et al., 2011).

Methods to characterize site networks based on animal movement fall into two main categories: empirical (or ‘functional’) and modelled (or ‘potential’) connectivity (Rayfield et al., 2011). Empirically derived connectivity infers site use and linkage from data on presence and movement, respectively (e.g., observed relocations of a marked individual at different sites; Martín-Vélez et al., 2020; Nightingale et al., 2023). In lieu of observational data, models have been used to estimate the probability of movement between sites, relying on various behavioural assumptions (e.g., migratory step distances; Xu et al., 2020), or expert opinion (Iwamura et al., 2013).

Migratory site networks based on modelled movements have been used to identify important sites for waterfowl and assess their spatial coverage by protected areas (Deboelpaep et al., 2022; Xu et al., 2020). Yet, it remains unclear whether network approaches based on empirical movement data are feasible at the flyway scale (but see Lamb et al., 2024), which may be an important step for achieving formal incorporation of connectivity metrics into important site assessments for migratory species (Davidson et al., 1999).

Over the centuries, numerous techniques have been developed to study the patterns and processes of avian migration (Bairlein, 2003). For determining site-level connectivity, techniques providing spatiotemporal histories of individuals are essential. Individual marking with rings (or ‘bands’) has long been used to recognize re-encountered individuals and infer movement behaviour, with over 100 million birds ringed in Europe alone since the 19th century (Thorup et al., 2014). In recent decades, tracking technologies have led to innumerous discoveries regarding avian migration (Bridge et al., 2011), and proved useful for describing site connectivity at both local (Martín-Vélez et al., 2020) and continental scales (Lamb et al., 2024). Integrating tracking data and ring re-observation data can improve inference of migratory patterns (Korner-Nievergelt et al., 2017), however this has yet to be applied to characterizing migratory site networks for migratory birds.

Here, we quantify site-level connectivity based on empirical evidence of individual-level movements of a migratory shorebird, the Black-tailed Godwit (*Limosa limosa*; hereafter, godwit), within the East

Atlantic Flyway, connecting western Europe and Africa. First, we assess the contributions of multiple sources of movement data to characterising the site network, leveraging metal-ring recoveries, colour-ring re-sightings, and tracking data, and then evaluate geographic variation in sampling completeness throughout the flyway. Next, we use the resulting networks to highlight sites of particular importance for godwits, in terms of connectivity. Finally, we evaluate protected area coverage of the site network and identify whether the most highly connected sites are formally recognized as important sites for the species. Overall, we aimed to assess the value of existing empirical movement data for identifying important connectivity sites for migratory species and thereby contributing to conservation policy and practice.

Materials and methods

Study species and populations

The Black-tailed Godwit is a medium-sized shorebird which breeds in wet grasslands from Northwest Europe to Northeast Asia (Zhu et al., 2021) and is considered Near-Threatened, due to ongoing population declines in parts of the flyway (BirdLife International, 2017). Here, we focused on the godwit populations within the East Atlantic Flyway. Godwits in this flyway are of three different populations with two subspecies, Icelandic breeders (*L. l. islandica*), western continental breeders (*L. l. limosa*; from Germany west) and eastern continental breeders (*L. l. limosa*; east of Germany). International coordination of conservation action for these three populations is covered in a Single Species Action Plan under the African-Eurasian Waterbird Agreement (Jensen et al., 2008). For the analysis, we treat these three populations together to provide a flyway-level perspective.

Movement data

We aimed to establish site-level connectivity via empirical evidence of individual movements. To maximize available information on godwit movements, we used data from three individual marking methods: metal-ring recoveries, colour-ring re-sightings, and satellite tracking (i.e., Platform

Transmitter Terminal [PTTs] and Global Positioning System transmitters [GPS]). Metal ring recoveries were acquired from the EURING Data Bank (Accessed June 6, 2022, du Feu et al., 2016), and colour-ring re-sightings and electronic tracking data directly from project coordinators (Table S1, Fig. S1).

Data preparation, combination, and filtering

To prepare the three datatypes for integration, we applied several filters. First, due to an apparent peak in the histograms of maximum displacement distribution across individuals, we removed individuals only recorded as travelling < 50 km from the initial marking location to reduce spatial bias Fig. S2).

Recoveries and re-sightings

Observations from the EURING data bank represent any observation of a ringed bird, living or dead. We obtained observations from 1980 to 2022, to which we applied a series of filters to retain observations of birds that were either caught, re-sighted in the field, or shot during hunting. Re-sightings of colour-marked godwits are further managed by scheme co-ordinators; we were able to collate data from 14 colour-mark schemes marking godwits in 9 countries (Table S1, Fig. S1). We excluded all observations in the EURING data also found in the colour-mark databases.

Tracking data

For tracking data, we excluded class ‘Z’ locations (PTT only) and applied a ground speed filter to remove unrealistic locations (PTT and GPS), with the maximum threshold set at 145 km/h (Senner et al., 2018). To reduce the influence of variation in sampling interval across individuals we regularized the tracking data to match the highest minimum interval across individuals of 6 h (Table S2), and tested the sensitivity of our results to this parameter (Supplementary Methods 1, Table S3, Fig. S3). Next, we identified and retained only periods of stationarity, defined as intervals of >=24 h within a site (see Site Definition sub-section below).

Data analysis

Network analysis

To quantify connectivity, we used network analysis, in which a ‘network’ is a mathematical representation of a system, composed of stationary nodes potentially connected via links (or ‘edges’; Jacoby and Freeman, 2016). We built unipartite, weighted, and directed networks to represent sites used by godwits and connected via their movements with the R package *sfnetworks* (Meer et al., 2023).

Defining sites and links

An important step in constructing migratory site networks is defining what constitutes a site (i.e., nodes in the network). We used Important Bird and Biodiversity Areas (hereafter ‘IBAs’) as our initial layer of potential sites (BirdLife International, 2022), as this allowed us to directly relate bird locations to specific, management relevant locations in the landscape. We then assigned bird relocations to an IBA if they fell inside or within 10 km of a site and tested the sensitivity of our results to this threshold (Table S3, Fig. S3). Relocations falling outside IBA buffers were assigned to a hexagonal grid cell of average cell-centre distance of 10 km. Adjacent hexcells with godwit relocations were then aggregated to form new, ‘non-IBA’ sites. To identify broad-scale spatial patterns in the contribution of each datatype (i.e., metal-ring recoveries, colour-ring re-sightings, and tracking) from West Africa to Northern Europe, sites were grouped into four latitudinal bands evenly spaced by 15° , based on location (<23°N, 23°N–38°N, 38°N–53N °, >53°N).

Links between sites were defined based on sequential relocations of an individual occurring within 20 days of a previous record (Fig. S4). This threshold was selected to represent ‘directed’, short-term movements as closely as possible while maximizing the inclusion of ring-based re-observations, which vary more widely in temporal resolution than tracking (Fig. S4). Alternative temporal thresholds were tested (5, 10, 15 and 25 days), and had little effect on the results (Table S3, Fig. S3).

Season definition

As the movement routes of migratory species often vary across seasons, we defined networks separately for two periods. The ‘post-breeding’ period was defined as June–October, to capture the period during which godwits end breeding and travel south, and the ‘pre-breeding’ period was defined as November– May, to encompass the entire period of northward movements (Verhoeven et al., 2021).

Connectivity metrics

To assess the relative importance of sites in terms of connectivity, we used two classical centrality metrics from network analysis: in-strength and weighted betweenness. In-strength is the weighted version of the in-degree, i.e., the number of links into a site (Rayfield et al., 2011), calculated by summing the weights (see below) of links directed into a site. In-strength thereby provides a measure of the importance of a site as an ‘arrival hub’. The betweenness is the number of shortest paths passing through a focal site. When links are weighted, the ‘distance’ between sites is a determined by link weight, with shortest paths calculated using the Dijsktra algorithm (Opsahl et al., 2010). Weighted betweenness measures how much a site acts as a ‘steppingstone’ between sub-sections of the network, considering the strength of connection between sites (Rayfield et al., 2011).

Link weights

Link weights were set to represent the strength of connection between two sites in terms of the number of birds observed forming the link:

$$w_i = (r_i + t_i)/2$$

Where the weight w of link i represents the mean of the ring-based weight (r_i: the sampling-effort adjusted (see below) proportion of all individuals observed from rings forming the link) and the tracking-based weight (t_i: the proportion of all tracked individuals observed forming the link). As the total number of birds relocated from ringing and tracking differ, each datatype-specific weight was re-scaled by dividing by their maximum values (i.e., max[r_i], max[t_i]). For links identified from only one or the other datatype, the available datatype was used alone to set the link weight. As metal-ring recovery data contribute relatively little data on links (<1%, Table 1, Fig. S4), we opted to combine these data with colour-ring re-sightings for this step.

The detection probability of a ringed bird varies spatially, due in part to variation in observer effort (Thorup et al., 2014). To account for this, we adjusted ring-based link weights (r_i) based on the estimated degree of observer effort in each country, where links formed from observations in less sampled countries were up-weighted, and those from highly sampled countries down-weighted (Supplementary Methods 2; Fig. S5, Table S4).

Sampling curve analysis of network structure

To assess spatial patterns in the sampling completeness of network elements (i.e., sites and links) across the flyway, we used a randomized sampling curve analysis (Supplementary Methods 3). For each country in the network with at least 15 unique bird-site observations (N = 26), we drew random samples of a progressively increasing number of observations and counted the number of sites and links they contributed for that country, independent of season. We repeated this procedure 1000 times and then plotted the curve formed between sample size (N observations) and network elements (N sites or N links). We then fitted a linear model between the number of network elements identified and the sample sizes at the top of each curve (i.e., the five highest sample sizes). We took the slope of each country-model to indicate the amount of information added by additional sampling in that country, i.e., the number of sites or links identified per bird-site observation, after considering all sampling effort. As with classic species-sampling curves, we expect the slope to be steep at low sampling levels and slow as sampling increases, when only rarely used sites or links are observed (Bunge and Fitzpatrick, 1993). Finally we fitted linear models between country-curve slopes and the latitude and longitude of country centroids respectively to identify spatial patterns.

Bootstrapping and top connectivity sites

To reduce the effect of sampling bias and quantify uncertainty of the network metric estimates, we utilized a bootstrapping approach to construct networks. Across 7500 iterations, we drew samples (with replacement) of 10,269 (pre-breeding) and 9274 (post-breeding) birds and re-constructed the network. As the deployment of tracking devices is spatially uneven (Fig. S1), we drew equal-sized samples from different countries to equalize their influence on the network (Supplementary Methods 4). In each iteration, we calculated the in-strength and weighted betweenness for each site. We then calculated the bootstrap median of in-strength and weighted betweenness and ranked each site. We next identified the 'top sites' using a percentile threshold of the bootstrap metric value across all sites, determined by plotting the bootstrap metric value against site rank and identifying an inflection point in the curve (Xu et al., 2020). Finally, we determined the stability of top site designation as whether the interquartile range (IQR) of the site's metric value was above the cut-off threshold value (as defined above).

Protected area coverage and IBA congruency

We overlaid all sites, irrespective of season, on the aggregated polygons of the World Database on Protected Areas (www.protectedplanet.net, download date: October 2022) to calculate the proportion of godwit sites covered by protected areas (excluding UN Biosphere reserves), and the percentage of relocations associated with a site falling within protected areas. Finally, we assessed the number of top sites that are IBAs with (1) godwits or (2) 'waterbirds' in general as the trigger taxa (i.e., those which meet thresholds of importance and therefore contribute to the sites qualification), and (3) sites not recognized as IBAs (BirdLife International, 2022).

Results

Seasonal networks and datatype contributions

In total, we collated data from 29,997 individual birds from 1980 to 2023. After filtering, 10,701 birds remained, contributing a total of 434,996 observations (Table 1), 89% of which were collected from 2010 to 2023 (Fig. S6).

Across the three datatypes, 10,269 and 9274 individual birds contributed information to identify sites during the pre-breeding (November–May) and post-breeding (June–October) periods, respectively (Table 1). We identified 1058 sites used by godwits, of which 803 were used during pre-breeding and 734 during post-breeding (Fig. 1A). Overall, re-sightings of colour-marked birds contributed the largest number of sites (70%), followed by tracking (50%) and metal ring recoveries (25%; Fig. 1B). There was a clear latitudinal pattern in the relative contribution of each datatype, with colour-ring re-sightings contributing more site information in the north of the range (>38°N) and tracking being the predominant source in the south (<38°N; Fig. 1C).

Direct link information (i.e., subsequent relocations at separate sites within 20 days) was contributed by 8742 birds during pre-breeding and 6088 birds during post-breeding (Table 1), resulting in 2695 unique links between sites during pre-breeding and 2015 unique links during post-breeding (Fig. 2). Colour-ring re-sightings contributed the highest number of links during pre-breeding (60%), followed by tracking (49%) and metal-ring recoveries (0.6%). During post-breeding, tracking contributed the most link information (63%), followed by re-sightings (43%) and recoveries (0.4%; Fig. 2). Each site was directly linked to a median of 2 (min=0, max=181) other sites during pre-breeding and to 2 (min=0, max=131) other sites during post-breeding.

Sampling and network structure

The slope of sampling curves of both sites and links increased with longitude, indicating a decline in sampling completeness from west to east (Fig. 3, Table S5). For sites, curve slopes were near zero (i.e., < 0.01 new sites are identified per observation) for 10 countries (39%; n=26; Fig. S7), while new link identification remained high for most countries (median slope: 0.41, range: 0.68 –1, Fig. S8). Across each seasonal network 30% and 27% of sites lacked direct link information, for pre-breeding and post-breeding, respectively, with countries sampled predominantly with ring-based data (re-sightings and recoveries) having a higher percentage of disconnectedness (Fig. S9).

Top connectivity sites

We used the 97th percentile of the in-strength and weighted betweenness metrics as cut-offs to identify top connectivity sites, resulting in a total of 49 sites, 35 for pre-breeding and 32 for post-breeding, with 18 being top sites in both seasons (Fig. 4, Table S3). We found 67% (33 of the 49) of top sites to be stable (i.e., the IQR of a site's bootstrap centrality metric did not include the top site cut-off value), with 69% (24 of 35) and 75% (24 of 32) being stable for pre-breeding and post-breeding respectively (Table S6).

Top sites were in 12 different countries, from Guinea-Bissau in the south to Iceland in the north, led by the Netherlands (9), Senegal (7), and France (7). On average, top sites were directly linked to 48 other sites (median, IQR 32–84), and 8 other countries (median, IQR 6–10), with three sites linked to >200 other sites: Guadalquivir marshes (Spain), Tagus estuary (Portugal) and Wonseradeel & Workum (Netherlands), and an additional six linked to >100 other sites (Table S6). Of all 49 top sites, 9 (18%) are sites where birds have been tagged with tracking devices, 27 (55%) where birds have been ringed, and 22 (45%; mostly in Africa) are neither ringing nor deployment sites for tracking (Table S6).

Protected area coverage and IBA status

Considering all sites, 80% had some spatial overlap with protected areas (Fig. 5A) with a mean of 44% (+/- SD 44%) of bird relocations falling within protected areas. Of the 49 top sites identified, 6 (12%) had no spatial coverage by protected areas, 23 (47%) had godwits as a trigger species underlying their IBA status, a further 21 (43%) had 'waterbirds' listed as a trigger group, and 5 sites (10%) are not IBAs (Table S6). The five non-IBA sites were in the Inner Niger delta of Mali (1), the upper Senegal River basin of Senegal and Mauritania (2), southern Senegal (1) and Guinea-Bissau (1; Fig. 5B).

The network perspective tool

Our results are accessible in a Shiny app (https://bit.ly/3WOdinm) which facilitates viewing the connectivity of (1) a focal site, (2) all sites in a country, or (3) between a pair of countries (Fig. 6).

Table 1 Summary of Black-tailed Godwit relocation data illustrating the number of individuals birds (N birds) and relocations (N points) for three different datatypes, before and after filtering. The data are further split to show the quantity of data available for identifying sites and links for each seasonal network after filtering.

	pre-filter		**post-filter**			**sites**		**links**	
datatype	**N birds**	**N points**	**N birds**	**N points**	**season**	**N birds**	**N points**	**N birds**	**N points**
colour	14,117	281,729	9928	263,097	Jun – Oct	7878	74,053	5604	65,169
					Nov – May	9318	188,603	8300	185,377
metal	3922	14,227	1765	8147	Jun – Oct	858	3465	507	2719
					Nov – May	1275	4673	1039	3471
tracking	468	158,439	390	121,266	Jun – Oct	370	59,138	355	58,894
					Nov – May	357	62,128	305	60,401
total	29,997	481,803	10,270	261,867	Jun – Oct	9274	139,980	6088	129,091
					Nov – May	10269	261,854	8742	255,247

Fig. 1 Sites used by Black-tailed Godwits in the East Atlantic Flyway. Colours in each panel indicate the datatype(s) that identified a site. (A) Location of all 1058 sites. (B) The proportion of all sites identified by each datatype combination and (C) with sites grouped into equal-sized latitudinal bands.

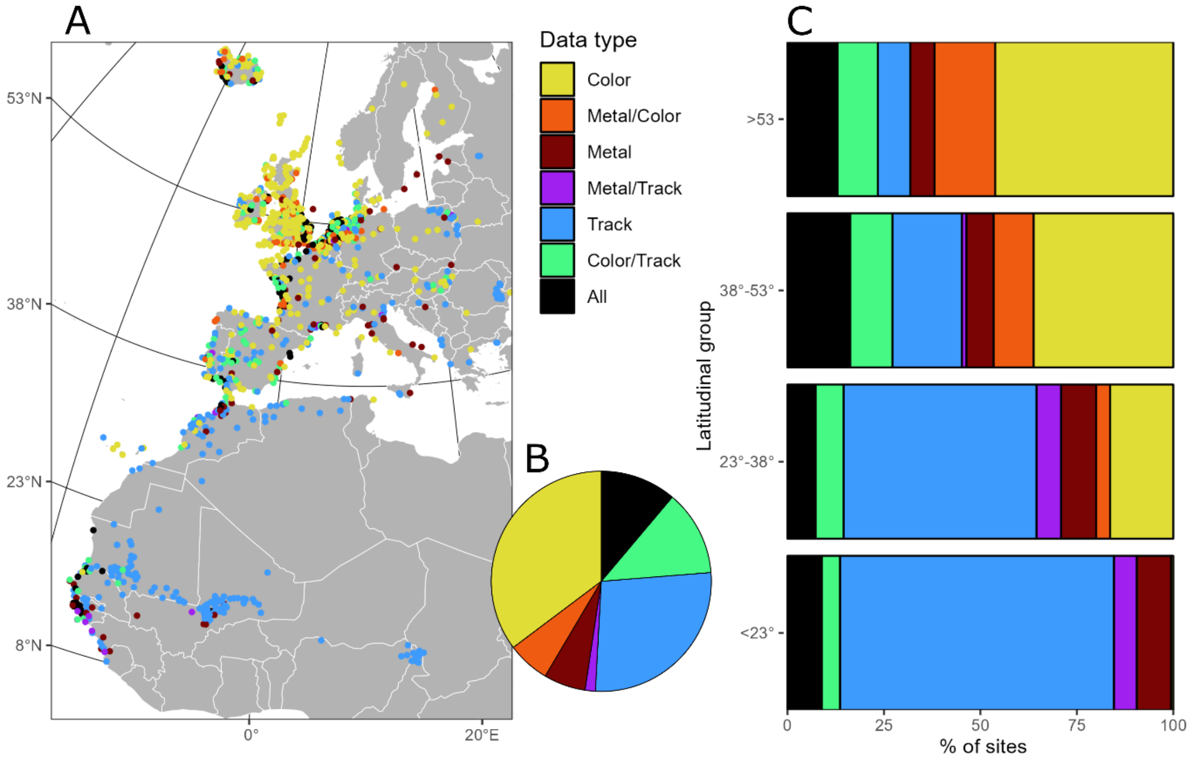


Fig. 2 Links between sites used by Black-tailed Godwits during pre-breeding (November–May; left) and post-breeding (June– October; right). Each link signifies the sequential occurrence of ≥1 godwit at two sites within 20 days. Line colour indicates the datatype combination that identified the link. Inset pie charts show the proportion of links identified by each datatype; lines are plotted in order of most (bottom) to least (top) abundant datatype per season.

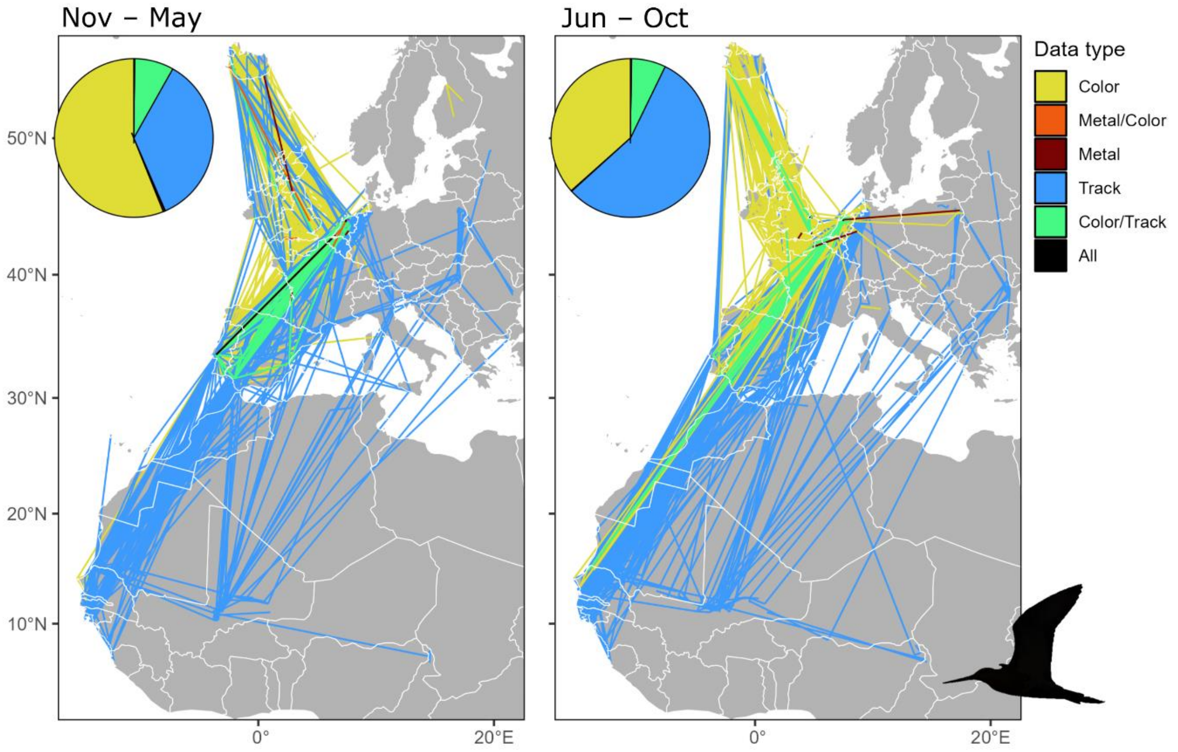


Fig. 3 Sampling completeness of sites (A) and links (B) as a function of geography. Randomized sampling curves were estimated for each country by iteratively re-drawing bird-observation samples of increasing size and counting the sites or links identified. The slope across the five-highest sample sizes was taken as a measure of sampling completeness, where a steep slope indicated rapid information gain (lower completeness) and a flat slope indicated high information redundancy (more complete). Lines (A, B) represent the predicted effect of linear models of country longitude (centroid) on sampling curve slope, and shaded areas indicate +/- 1 SE. The model prediction (A) was back-transformed from the square root scale. Right-hand panels show example curves of two countries with contrasting slopes in the western (Portugal) and eastern (Poland) part of the flyway, for sites (top two) and links (bottom two).

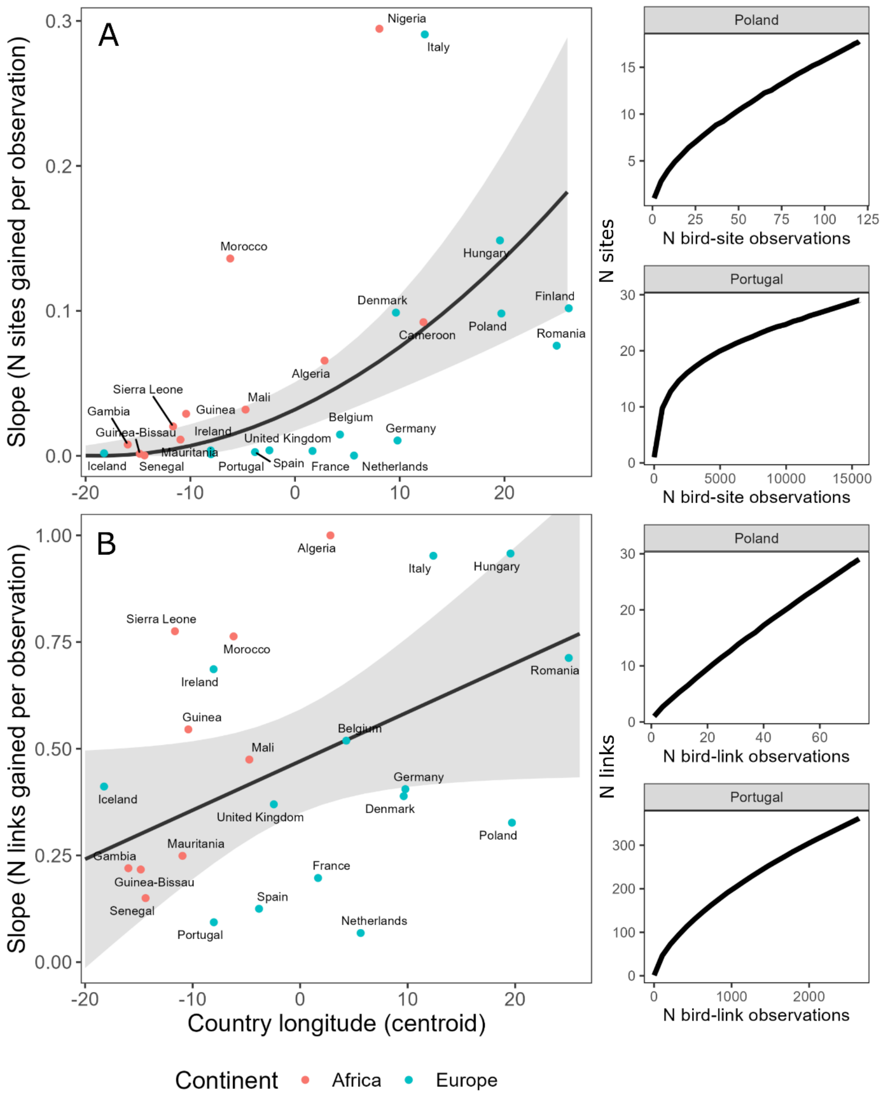


Fig. 4 Top connectivity sites during pre-breeding (November–May; A-D) and post-breeding (June–October; E-H). Top sites identified using (A,E) in-strength (weighted sum of links directed into the site), and (C,G) weighted betweenness (number of shortest paths in the network passing through the focal site, where path lengths are the sum of link weights). (B,D,F,H) All sites ranked by network metrics against their bootstrap median metric value calculated across 1000 iterations of network construction; grey bars indicate the interquartile range. The dashed line indicates the threshold (97%), above which sites are considered top connectivity sites.

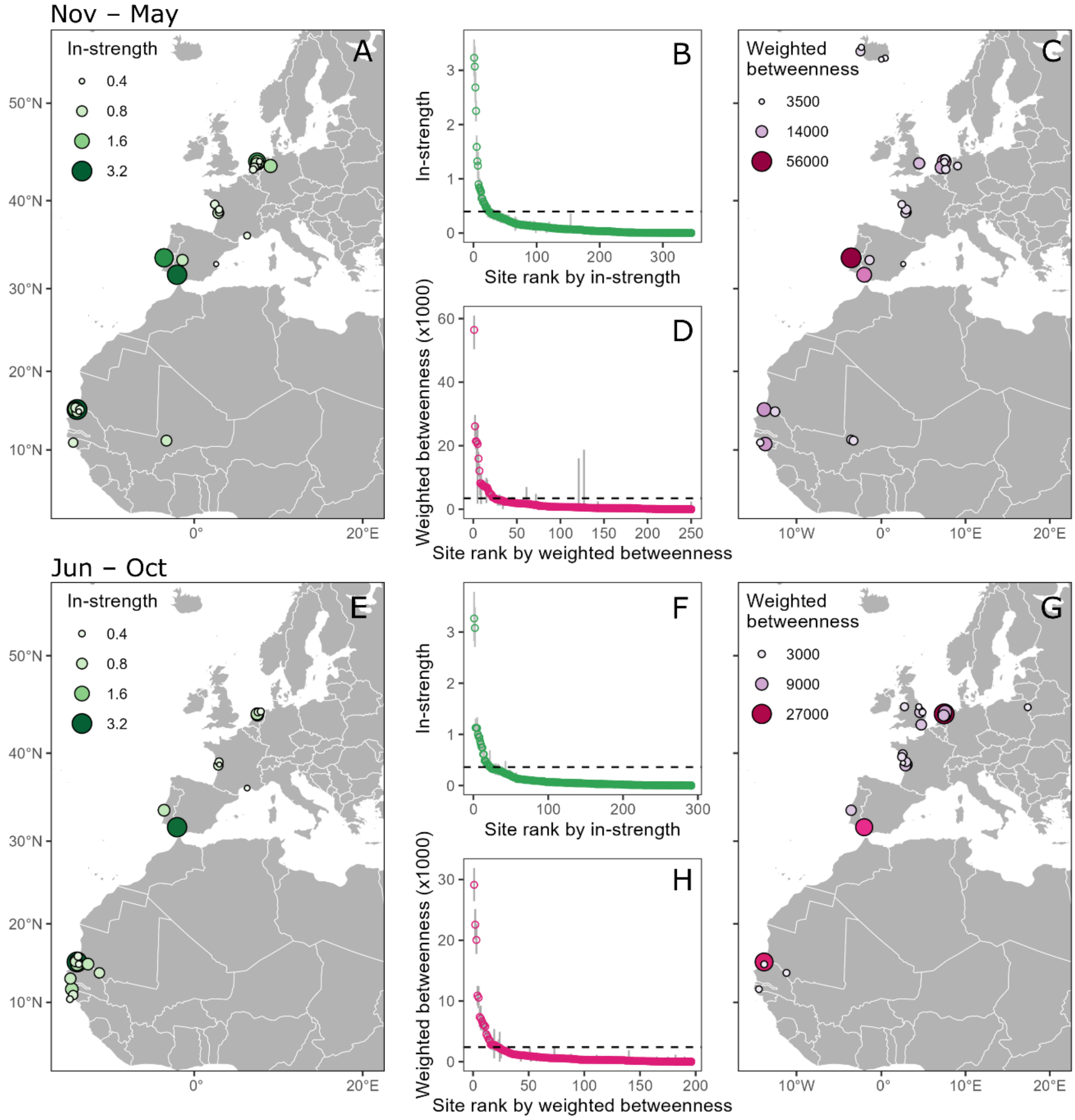


Fig. 5 Conservation designation of sites in the migratory site network of Black-tailed Godwits. (A) Spatial coverage by protected areas. (B) Recognition of top connectivity sites as Important Bird and Biodiversity Areas. Sites are classified as either Godwit IBAs (recognized as important for the species in particular), Waterbird IBAs (important for waterbirds generally), or non-IBAs.

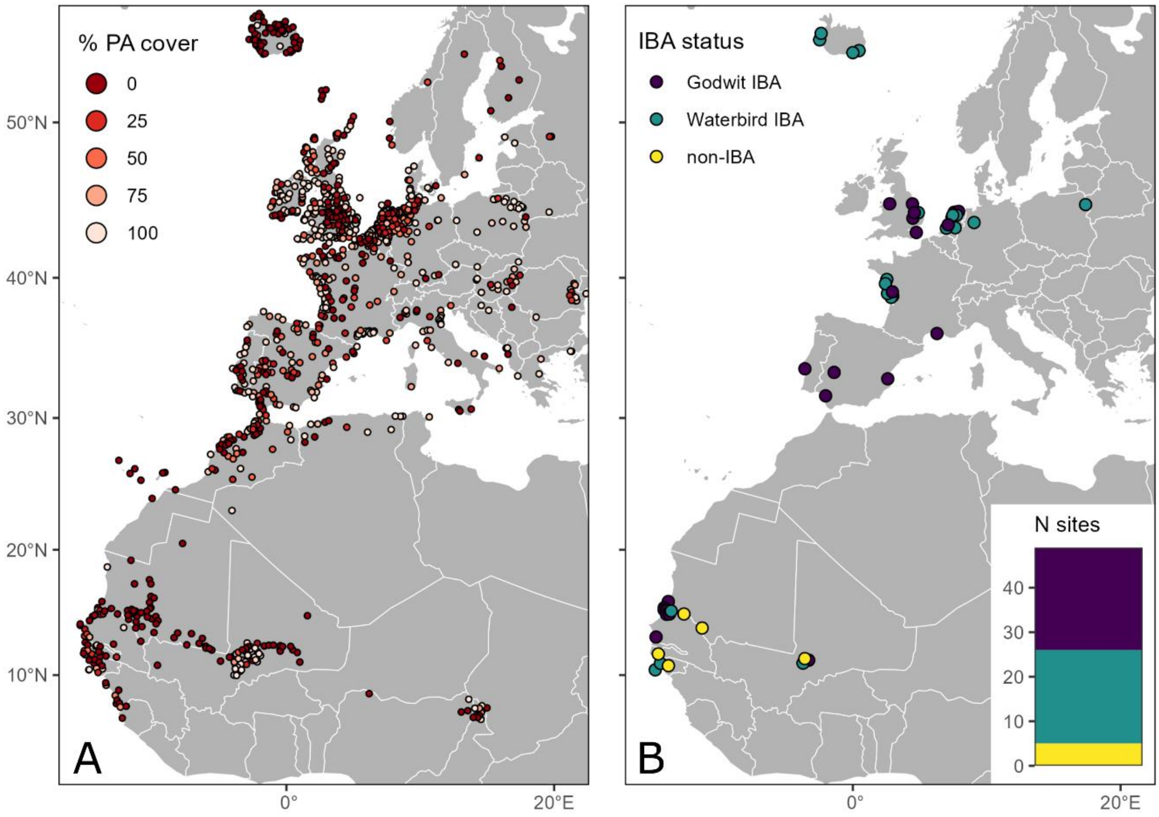
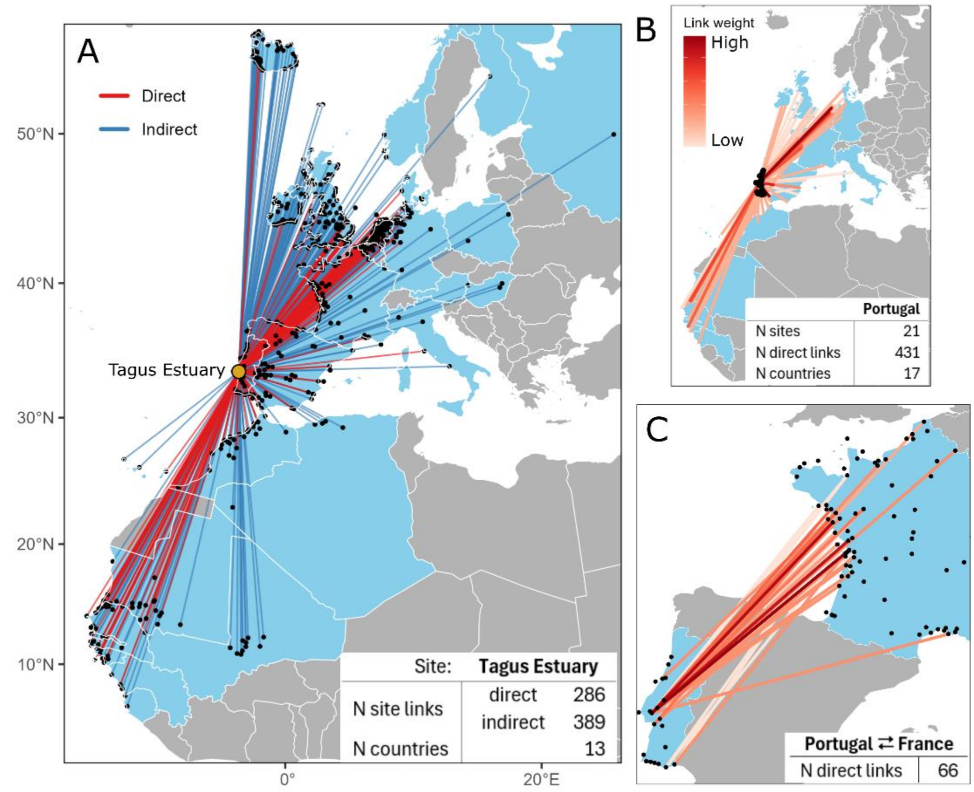


Fig. 6 Examples of how parts of the Black-tailed Godwit migratory site network can be visualized from different perspectives. (A) Direct and indirect connectivity for a focal site (Tagus Estuary, Portugal). Direct links are subsequent relocations of an individual within 20 days, and indirect links include all places godwits observed in the Tagus were also recorded. (B) Direct connectivity into or out of all sites in Portugal during pre-breeding (November–May). (C) Direct links during pre-breeding between sites in two countries, Portugal and France. An interactive version of this figure and underlying tables can be found at https://bit.ly/3WOdinm



Discussion

We characterized site networks for the seasonal migration of Black-tailed Godwits in the East Atlantic Flyway, using three sources of individual-level movement data (Fig. 1-2) mostly collected during the last decade. These data, and the extensive efforts behind their collection, allowed us to reveal links between sites across the entire flyway (Fig. 2). Our results indicate that although sampling of site-level connectivity for this species is still incomplete, particularly in the eastern part of the flyway (Fig. 3), it was possible to pinpoint a small number of sites that were especially important in the network (Fig. 4). Most of these sites appear robust to uncertainty related to sampling (Table S6) and several are not covered by existing area-based management measures (Fig. 5). Such empirical demonstrations of site connectivity can facilitate integration of connectivity metrics in conservation processes and practice, and ultimately improve spatial protection for migratory species.

Broader data input improves network

We found clear regional variation in datatype contributions to the network structure, reflecting historical and geographical patterns of godwit research across the flyway (Fig. 1-2). Considerable effort has been put into all three sampling methods in the West European range of continental godwits (Kentie et al., 2016; Verhoeven et al., 2021), proportionally higher effort put into ring-based methods to study Icelandic godwits (Gunnarsson et al., 2005), and less overall investment in godwit research in eastern Europe and Africa. By integrating these efforts, we gained an improved picture of the network and the key sites within it. If we had solely based our analysis on tracking data, 504 sites (48%) and 2299 links (54%) would have been missed, principally in the UK, Ireland, and Iceland. Likewise, using solely colour-ring re-sightings would have excluded 368 sites (29%) and 2095 links (51%), particularly in West Africa.

Simulations indicate that spatial heterogeneity in the sampling of a migratory population can impact inference of population-level connectivity (Vickers et al., 2021). Our sampling curves show that the structure of the network is better resolved in the west of the godwit range, with movement information lacking further east (Fig. 3). To ameliorate differences in sampling effort across countries, we adjusted the relative influence of links. This approach cannot account for the non-detection of a site or link; however, it is unlikely that sites within the top 3% of either connectivity metric would be undetected. This is analogous to community richness sampling, in which the ‘generalist core’ is identified first, followed by the ‘specialist tail’, which requires more sampling to resolve (Henriksen et al., 2019). Our estimates of the completeness of site and link identification per country could help identify priority areas for future movement sampling of godwits, e.g., in countries like Hungary or Poland (Fig. S7–8; Loonstra et al., 2020).

Our results show that it is feasible to characterize site networks at the flyway scale using empirical movement data. When possible, basing assessments of site importance on empirical data may be preferable to estimating connectivity based on e.g., dispersal distances, which risks overlooking population-specific connectivity patterns. Hybrid connectivity approaches, e.g., identifying sites from occurrence data and modelling potential links (Xu et al., 2020) are promising but largely untested. Direct comparisons between empirical and theoretical approaches could help determine the circumstances in which modelling of connectivity could be used when sufficient movement data are not yet available.

Added value to important site identification

Priority site standards are a common way in which areas are assessed for their ecological importance; however, assessments often only consider sites in isolation. For example, important sites for migratory waterbirds, such as the Ramsar Convention’s Wetlands of International Importance, are often identified based on standardized counts performed once a year, which may underestimate the importance of sites used outside the count period or with high bird turnover (Navedo and Piersma, 2023; Vervoort et al., 2022). Connectivity approaches such as ours provide a way of quantifying the importance of such sites across the full annual cycle. Indeed, of the 34 top connectivity sites we identified in countries where godwits spend the non-breeding season, 21 (62%) are either outside the top 34 sites in terms of the maximum number of godwits reported there at mid-winter counts performed since at least 1990, or lack count information entirely (Table S6, Wetlands International, 2023).

The top sites we identified play a critical role in connecting the various locations godwits use throughout the annual cycle. Five sites identified in West Africa lack formal recognition of their importance for waterbirds, and a further 21 sites throughout the flyway are unrecognized as important to Black-tailed Godwits specifically (Table S6), suggesting our method adds value to existing efforts. Although the importance of areas in e.g., eastern Britain (for Icelandic godwits) or Guinea-Bissau (for continental godwits) has been previously described (Alves et al., 2012; Verhoeven et al., 2021), quantifying their key role in linking sites across the flyway (e.g., as widely-used hubs and/or steppingstone sites) represents novel insight only possible within a unified framework.

A strength of our approach is that the site network can be readily disaggregated to answer questions about the relative (e.g., who are ‘we’ connected to?) importance of a particular site or region (e.g., Fig. 6A-B). Demonstrating the degree of connectivity of a site can be particularly helpful in the face of disruptive development. For example, data on the connectivity of birds using the Tagus Estuary provided crucial evidence of this site’s importance, leading to a re-evaluation of an airport development proposal (Alves and Dias, 2020; Nightingale et al., 2023). As continental godwit populations are in severe decline, any loss of key sites, such as the Tagus Estuary or the Guadalquivir marshes (Doñana), could cause cascading effects across the network, reducing the options available to the birds during the non-breeding period (Gill et al., 2007; Vansteelant, 2023). Site network analyses, such as ours, can be useful for evaluating scenarios of loss or degradation of sites due to sea-level rise, drought, or agricultural intensification (Iwamura et al., 2013), all of which are pervasive threats both for godwits and wetland biodiversity in general.

Conclusions

Integrating different sources of movement data, we evaluated and ranked site importance in terms of connectivity across the annual cycle of the Black-tailed Godwit. While many top connectivity sites are already recognized as important places for waterbirds, we identified several (mainly in West Africa) lacking recognition and any form of legal protection, highlighting the potential of our method to identify important sites missed by count-based methods. Our approach also extends previous efforts to characterize site networks for migratory birds by using empirical evidence of individual movements, rather than simulating bird behaviour from a restricted set of assumptions. As the recognition of ecological connectivity continues to grow in conservation policy and practice, robust methods to measure and compare it across regions and populations will become increasingly important.

Acknowledgements

To all black-tailed godwit ringers and observers that have contributed to catching operations and/or by reporting of rings or deploying of tracking devices. Thanks to the European Union for Bird Ringing (EURING) which made the recovery data available through the EURING Data Bank and to the many ringers and ringing scheme staff involved. We thank Stephane Guenneteau and Vincent Lelong, and Perrine Dulac and Jean Guy Robin for investments in the French breeding area of the Marais Breton, and Angela Helmecke for establishing the NABU colour-ringing programme in Schleswig-Holstein, Germany. Project Godwit is a partnership between RSPB and WWT with major funding from the EU LIFE Nature Programme and Natural England (LIFE15/NAT/UK/000753). Tracking and colour ringing in Lower Saxony was funded by the European Union and the Ministry of Environment of Lower Saxony (LIFE10 NAT/DE/011, LIFE19 IPE/DE/00004). Research by the University of Groningen team has been funded in 2020-2025 by the Ministry of LNV, Vogelbescherming Nederland (VBN), Provinces Fryslân, Overijssel, Groningen, Gelderland, Noord-Holland, Zuid-Holland, EU LIFE IP GrassBirdHabitats and the University of Groningen and builds on research funding in 2004-2019 by the Ministry of LNV, the Ministry of Economic Affairs, the Province of Fryslân, the Netherlands Organization for Scientific Research (NWO) for the TOP grant "Shorebirds in space" and the 2014 Spinoza Premium to T. Piersma, and by contributions from the University of Groningen, VBN, and World Wildlife Fund to the Chair in Global Flyway Ecology at the University of Groningen, large anonymous donations, the Gieskes-Strijbis Fund, and by contributions from the Prince Bernhard Culture Fund (through It Fryske Gea) and the Van der Hucht De Beukelaar Foundation. Financial support to CESAM was provided by FCT/MCTES (UIDP/50017/2020+UIDB/50017/2020+LA/P/0094/2020), and to cE3c by BirdLife International, The Royal Society for the Protection of Birds (RSPB), and Vogelbescherming Nederland (VBN) under project 'EAFConnect'. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The authors report no conflicts of interest.

Author contributions

Martin Beal, Josh Nightingale, Nicola Crockford, Anna Staneva, José A. Alves, and Maria P. Dias conceived the ideas and designed methodology. Martin Beal analysed the data and led writing of the manuscript. José A. Alves, João R. Belo, Chris Batey, Heinrich Belting, Pierrick Bocher, Malcolm Burgess, Taylor B. Craft, Philippe Delaporte, Lynda Donaldson, Guillaume Gélinaud, Jennifer A. Gill, Tómas G. Gunnarsson, Böðvar Þórisson, Jorge S. Gutiérrez, Jos C.E.W. Hooijmeijer, Ruth A. Howison, Philip Hunke, Loïc Jomat, Hilger Lemke, Jürgen Ludwig, Frank A. Majoor, Christopher Marlow, José A. Masero, Johannes Melter, Ian Nicholson, Josh Nightingale, Manuel Parejo, Barry O'Mahony, Esko Pasanen, Jorma Pessa, Theunis Piersma, Afonso D. Rocha, Frederic Robin, Maja Roodbergen, Pierre Rousseau, Volker Salewski, Luis Schmidt, Jennifer Smart, T. Lee Tibbitts, Sami Timonen contributed substantially to data collection, curation, and/or pre-processing. All authors contributed critically to the drafts and gave final approval for publication.

Statement on inclusion: Our study brings together authors from many different countries from across the region of study. In addition to the authors, many external stakeholders from around the world were engaged early on to ensure that the diverse sets of perspectives were considered.

Data availability statement

The tracking data analyzed in this study are available in Movebank (https://www.movebank.org/) under the following study IDs: 1923591036, 1693518103, 325569416, 49547785, 69402287, 75360602, 76429224, 163516781, 170829089, 175328223, 282596404, 293970900, 484019425, 652989041, 831990025, 878914763, 1105026166, 1145538280, 1183466126, 1482505185, 1482506572, 1487044886, 1498143083, 1563249841, 1658294759, 1693518103, 1751337831, 2083443328, 2098519852 and ring recovery records are available upon request from the Euring Data Bank (https://euring.org/). All data derivatives and analysis code produced by this study will be made openly available in a Zenodo repository upon publication.

References

Alerstam, T., 1993. Bird Migration. Cambridge University Press.

Alves, J.A., Dias, M.P., 2020. Portugal's airport plans threaten wetlands. Science 369, 1440–1440. https://doi.org/10.1126/science.abe4325

Alves, J.A., Gunnarsson, T.G., Potts, P.M., Gélinaud, G., Sutherland, W.J., Gill, J.A., 2012. Overtaking on migration: does longer distance migration always incur a penalty? Oikos 121, 464–470. https://doi.org/10.1111/j.1600-0706.2011.19678.x

Bairlein, F., 2016. Migratory birds under threat. Science 354, 547–548. https://doi.org/10.1126/science.aah6647

Bairlein, F., 2003. The study of bird migrations – some future perspectives. Bird Study 50, 243–253. https://doi.org/10.1080/00063650309461317

Beal, M., Oppel, S., Handley, J., Pearmain, E.J., Morera-Pujol, V., Carneiro, A.P.B., Davies, T.E., Phillips, R.A., Taylor, P.R., Miller, M.G.R., Franco, A.M.A., Catry, I., Patrício, A.R., Regalla, A., Staniland, I., Boyd, C., Catry, P., Dias, M.P., 2021. track2KBA: An R package for identifying important sites for biodiversity from tracking data. Methods Ecol. Evol. 12, 2372–2378. https://doi.org/10.1111/2041-210X.13713

BirdLife International, 2022. Important Bird and Biodiversity Area (IBA) digital boundaries: March 2022 version. BirdLife International, Cambridge, UK.

BirdLife International, 2017. Limosa limosa. IUCN Red List Threat. Species 2017. https://dx.doi.org/10.2305/IUCN.UK.2017-1.RLTS.T22693150A111611637.en

Bridge, E.S., Thorup, K., Bowlin, M.S., Chilson, P.B., Diehl, R.H., Fléron, R.W., Hartl, P., Kays, R., Kelly, J.F., Robinson, W.D., Wikelski, M., 2011. Technology on the Move: Recent and Forthcoming Innovations for Tracking Migratory Birds. BioScience 61, 689–698. https://doi.org/10.1525/bio.2011.61.9.7

Bunge, J., Fitzpatrick, M., 1993. Estimating the Number of Species: A Review. J. Am. Stat. Assoc. 88, 364–373. https://doi.org/10.1080/01621459.1993.10594330

Davidson, N., Bryant, D., Boere, G., 1999. Conservation uses of ringing data: Flyway networks for waterbirds. Ringing Migr. 19, 83–94. https://doi.org/10.1080/03078698.1999.9674214

Deboelpaep, E., Partoens, L., Koedam, N., Vanschoenwinkel, B., 2022. Highway(s) overhead: Strong differences in wetland connectivity and protected status challenge waterbird migration along the four Palearctic-Afrotropical flyways. Divers. Distrib. 28, 1067–1080. https://doi.org/10.1111/ddi.13508

DeLuca, W.V., Seavy, N.E., Grand, J., Velásquez-Tibatá, J., Taylor, L., Bowler, C., Deppe, J.L., Knight, E.J., Lentijo, G.M., Meehan, T.D., Michel, N.L., Saunders, S.P., Schillerstrom, N., Smith, M.A., Witko, C., Wilsey, C.B., 2023. A framework for linking hemispheric, full annual cycle prioritizations to local conservation actions for migratory birds. Conserv. Sci. Pract. 5, e12975. https://doi.org/10.1111/csp2.12975

Donald, P.F., Fishpool, L.D.C., Ajagbe, A., Bennun, L.A., Bunting, G., Burfield, I.J., Butchart, S.H.M., Capellan, S., Crosby, M.J., Dias, M.P., Diaz, D., Evans, M.I., Grimmett, R., Heath, M., Jones, V.R., Lascelles, B.G., Merriman, J.C., O'brien, M., Ramírez, I., Waliczky, Z., Wege, D.C., 2019. Important Bird and Biodiversity Areas (IBAs): the development and characteristics of a global inventory of key sites for biodiversity. Bird Conserv. Int. 29, 177–198. https://doi.org/10.1017/S0959270918000102

du Feu, C.R., Clark, J.A., Schaub, M., Fiedler, W., Baillie, S.R., 2016. The EURING Data Bank – a critical tool for continental-scale studies of marked birds. Ringing Migr. 31, 1–18. https://doi.org/10.1080/03078698.2016.1195205

Erickson, R.A., Diffendorfer, J.E., Norris, D.R., Bieri, J.A., Earl, J.E., Federico, P., Fryxell, J.M., Long, K.R., Mattsson, B.J., Sample, C., Wiederholt, R., Thogmartin, W.E., 2018. Defining and classifying migratory habitats as sources and sinks: The migratory pathway approach. J. Appl. Ecol. 55, 108–117. https://doi.org/10.1111/1365-2664.12952

Gill, J.A., Langston, R.H.W., Alves, J.A., Atkinson, P.W., Bocher, P., Cidraes Vieira, N., Crockford, N.J., Gélinaud, G., Groen, N., Gunnarsson, T.G., Hayhow, B., Hooijmeijer, J., Kentie, R., Kleijn, D., Lourenço, P.M., Masero, J.A., Meunier, F., Potts, P.M., Roodbergen, M., Schekkerman, H., Schröder, J., Wymenga, E., Piersma, T., 2007. Contrasting trends in two Black-tailed Godwit populations: a review of causes and recommendations. Wader Study Group Bull. 114, 43–50.

Gregory, K.A., Francesiaz, C., Jiguet, F., Besnard, A., 2023. A synthesis of recent tools and perspectives in migratory connectivity studies. Mov. Ecol. 11, 69. https://doi.org/10.1186/s40462-023-00388-z

Gunnarsson, T.G., Gill, J.A., Potts, P.M., Atkinson, P.W., Croger, R.E., Gélinaud, G., Gardarsson, A., Sutherland, W.J., 2005. Estimating population size in Black-tailed Godwits *Limosa limosa islandica* by colour-marking. Bird Study 52, 153–158. https://doi.org/10.1080/00063650509461385

Henriksen, M.V., Chapple, D.G., Chown, S.L., McGeoch, M.A., 2019. The effect of network size and sampling completeness in depauperate networks. J. Anim. Ecol. 88, 211–222. https://doi.org/10.1111/1365-2656.12912

IUCN, A., 2016. A global standard for the identification of key biodiversity areas, version 1.0.

Iwamura, T., Possingham, H.P., Chadès, I., Minton, C., Murray, N.J., Rogers, D.I., Treml, E.A., Fuller, R.A., 2013. Migratory connectivity magnifies the consequences of habitat loss from sea-level rise for shorebird populations. Proc. R. Soc. B Biol. Sci. 280, 20130325. https://doi.org/10.1098/rspb.2013.0325

Jacoby, D.M.P., Freeman, R., 2016. Emerging Network-Based Tools in Movement Ecology. Trends Ecol. Evol. 31, 301–314. https://doi.org/10.1016/j.tree.2016.01.011

Jensen, F.P., Béchet, A., Wymenga, E., 2008. International Single Species Action Plan for the Conservation of Black-tailed Godwit Limosa l. limosa & L. l. islandica. (No. 37), AEWA Technical Series. Bonn, Germany.

Kentie, R., Senner, N.R., Hooijmeijer, J.C.E.W., Márquez-Ferrando, R., Figuerola, J., Masero, J.A., Verhoeven, M.A., Piersma, T., 2016. Estimating the Size of the Dutch Breeding Population of Continental Black-Tailed Godwits from 2007–2015 Using Resighting Data from Spring Staging Sites. Ardea 104, 213–225. https://doi.org/10.5253/arde.v104i3.a7

Korner-Nievergelt, F., Prévot, C., Hahn, S., Jenni, L., Liechti, F., 2017. The integration of mark re-encounter and tracking data to quantify migratory connectivity. Ecol. Model. 344, 87–94. https://doi.org/10.1016/j.ecolmodel.2016.11.009

Lamb, J.S., Cooper-Mullin, C., Gilliland, S.G., Berlin, A.M., Bowman, T.D., Boyd, W.S., De La Cruz, S.E., Esler, D., Evenson, J.R., Flint, P., Lepage, C., Meattey, D.E., Osenkowski, J.E., Paton, P.W., Perry, M.C., Rosenberg, D., Savard, J.-P.L., Savoy, L., Schamber, J., Ward, D.H., Takekawa, J.Y., McWilliams, S.R., 2024. Evaluating conservation units using network analysis: a sea duck case study. Front. Ecol. Environ. n/a, e2648. https://doi.org/10.1002/fee.2648

Le Saout, S., Hoffmann, M., Shi, Y., Hughes, A., Bernard, C., Brooks, T.M., Bertzky, B., Butchart, S.H.M., Stuart, S.N., Badman, T., Rodrigues, A.S.L., 2013. Protected areas and effective biodiversity conservation. Science 342, 803–805. https://doi.org/10.1126/science.1239268

Loonstra, A.J., Verhoeven, M.A., Zbyryt, A., Schaaf, E., Both, C., Piersma, T., 2020. Individual Black-tailed Godwits do not stick to single routes: a hypothesis on how low population densities might decrease social conformity. Ardea 107, 251–261.

Martin, T.G., Chadès, I., Arcese, P., Marra, P.P., Possingham, H.P., Norris, D.R., 2007. Optimal Conservation of Migratory Species. PLOS ONE 2, e751. https://doi.org/10.1371/journal.pone.0000751

Martín-Vélez, V., Mohring, B., van Leeuwen, C.H.A., Shamoun-Baranes, J., Thaxter, C.B., Baert, J.M., Camphuysen, C.J., Green, A.J., 2020. Functional connectivity network between terrestrial and aquatic habitats by a generalist waterbird, and implications for biovectoring. Sci. Total Environ. 705, 135886. https://doi.org/10.1016/j.scitotenv.2019.135886

Meer, L. van der, Abad, L., Gilardi, A., Lovelace, R., 2023. sfnetworks: Tidy Geospatial Networks.

Navedo, J.G., Piersma, T., 2023. Do 50-year-old Ramsar criteria still do the best possible job? A plea for broadened scientific underpinning of the global protection of wetlands and migratory waterbirds. Conserv. Lett. 16, e12941. https://doi.org/10.1111/conl.12941

Nightingale, J., Gill, J.A., Þórisson, B., Potts, P.M., Gunnarsson, T.G., Alves, J.A., 2023. Conservation beyond Boundaries: using animal movement networks in Protected Area assessment. Anim. Conserv. n/a. https://doi.org/10.1111/acv.12868

Opsahl, T., Agneessens, F., Skvoretz, J., 2010. Node centrality in weighted networks: Generalizing degree and shortest paths. Soc. Netw. 32, 245–251. https://doi.org/10.1016/j.socnet.2010.03.006

Rayfield, B., Fortin, M.-J., Fall, A., 2011. Connectivity for conservation: a framework to classify network measures. Ecology 92, 847–858. https://doi.org/10.1890/09-2190.1

Runge, C.A., Watson, J.E.M., Butchart, S.H.M., Hanson, J.O., Possingham, H.P., Fuller, R.A., 2015. Protected areas and global conservation of migratory birds. Science 350, 1255–1258. https://doi.org/10.1126/science.aac9180

Senner, N.R., Stager, M., Verhoeven, M.A., Cheviron, Z.A., Piersma, T., Bouten, W., 2018. High-altitude shorebird migration in the absence of topographical barriers: avoiding high air temperatures and searching for profitable winds. Proc. R. Soc. B Biol. Sci. 285, 20180569. https://doi.org/10.1098/rspb.2018.0569

Sutherland, W.J., 1997. Predicting the consequences of habitat loss for migratory populations. Proc. R. Soc. Lond. B Biol. Sci. 263, 1325–1327. https://doi.org/10.1098/rspb.1996.0194

Thorup, K., Korner-Nievergelt, F., Cohen, E.B., Baillie, S.R., 2014. Large-scale spatial analysis of ringing and re-encounter data to infer movement patterns: A review including methodological perspectives. Methods Ecol. Evol. 5, 1337–1350. https://doi.org/10.1111/2041-210X.12258

UNEP-CMS, 2024. Resolution 14.16 (Rev.COP14) Ecological Connectivity. Samarkand, Uzbekistan.

UNEP-WCMC, 2024. State of the World's Migratory Species. UNEP-WCMC, Cambridge, United Kingdom.

Vansteelant, W.M.G., 2023. A godwit perspective on rapid wetland loss in Doñana and the Guadalquivir delta. Wader Study 130. https://doi.org/10.18194/ws.00315

Verhoeven, M.A., Loonstra, A.J., McBride, A.D., Both, C., Senner, N.R., Piersma, T., 2021. Migration route, stopping sites, and non-breeding destinations of adult Black-tailed Godwits breeding in southwest Fryslân, the Netherlands. J. Ornithol. 162, 61–76. https://doi.org/10.1007/s10336-020-01807-3

Vervoort, R., Schmaltz, L.E., Hooijmeijer, J.C.E.W., Verkuil, Y.I., Kempenaers, B., Piersma, T., 2022. Within- and between-Year Variation in the Presence of Individually Marked Ruff Calidris pugnax at a Stopover Site during Northward Migration. Ardea 110, 41–59. https://doi.org/10.5253/arde.v110i1.a1

Vickers, S.H., Franco, A.M.A., Gilroy, J.J., 2021. Sensitivity of migratory connectivity estimates to spatial sampling design. Mov. Ecol. 9, 16. https://doi.org/10.1186/s40462-021-00254-w

Wetlands International, 2023. IWC Online database. URL https://iwc.wetlands.org/index.php (accessed 8.2.23).

Xu, Y., Green, A.J., Mundkur, T., Hagemeijer, W., Mossad, H., Prins, H.H.T., de Boer, W.F., 2022. Beyond Site-Specific Criteria: Conservation of Migratory Birds and Their Habitats from a Network Perspective. Diversity 14, 353. https://doi.org/10.3390/d14050353

Xu, Y., Si, Y., Takekawa, J., Liu, Q., Prins, H.H.T., Yin, S., Prosser, D.J., Gong, P., de Boer, W.F., 2020. A network approach to prioritize conservation efforts for migratory birds. Conserv. Biol. 34, 416–426. https://doi.org/10.1111/cobi.13383

Zhu, B.-R., Verkuil, Y.I., Conklin, J.R., Yang, A., Lei, W., Alves, J.A., Hassell, C.J., Dorofeev, D., Zhang, Z., Piersma, T., 2021. Discovery of a morphologically and genetically distinct population of Black-tailed Godwits in the East Asian-Australasian Flyway. Ibis 163, 448–462. https://doi.org/10.1111/ibi.12890