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Conservation beyond Boundaries: using animal movement networks in Protected Area assessment

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Abstract

Protected areas (PAs) are a core component of conservation policy and practice. However, many species for which they are designated are highly mobile, and may move among sites within and beyond PA boundaries. Environmental impacts on sites beyond those boundaries could thus impact the PA's protected populations, with the risk of adversely affecting its conservation objectives. Conservationists therefore urgently need tools to assess impacts on PAs and their populations of developments beyond their boundaries. We present a framework for using network analysis of observations of marked individuals to assess the *protection footprint* of PAs in the wider landscape and the *impact footprint* of developments within or neighboring PAs. We illustrate the use of this framework by assessing the impact of a current airport development proposal on a partially protected wetland, the Tagus estuary in Portugal, specifically by evaluating the extent of noise disturbance on the PA's population of Black-tailed Godwits, a protected migratory wader species. By analyzing individual movements between sites and across seasons, we find disturbance impacts on up to 68.3% of individual Black-tailed Godwits overall, greatly exceeding the estimates of 0.46–5.5% in the airport's Environmental Impact Assessments which derived from count data. We then compared the pre-development network with simulated networks that represented two levels of site avoidance by removing sites predicted to receive noise in excess of two thresholds, 55 or 65 dB(A). Avoidance by Godwits of the potentially-impacted sites is predicted to have a larger effect on network structure than removing the same number of sites at random, suggesting that an airport in the proposed location would operate as a barrier to connectivity in this wetland. We also highlight the role that network analyses of locations of marked individuals can play in assessing environmental impacts on protected sites and populations.

Introduction

On a planet dominated by anthropogenic impacts on biodiversity, statutory protected areas (PAs) are a core component of conservation practice, targets and policy (Bhola *et al*., 2021). However, PAs frequently encompass only a subset of the sites (or habitats) used by individuals of the species intended for protection, for which the PA may have been designated. PAs, like all ecological systems, are open to flows of matter, information and organisms across their boundaries (Schiesari *et al*., 2019), and success in meeting their conservation objectives can thus depend on conditions in their unprotected surroundings (DeFries *et al*., 2007). Given the constraints that competing land uses often place on PA size and location, the need to ensure that PAs encompass important areas for target species, and the range of spatial scales over which individuals using PAs might move, conservationists are increasingly concerned with facilitating connectivity between separate PAs and with the surrounding landscape (Hilty *et al*., 2020), and understanding how development plans might disrupt such connectivity of PAs.

Designation of PAs is frequently based on the presence of particular species, often highly mobile animal species for which connectivity within and between PAs is likely to be particularly important. For example, the European Union (EU) Birds Directive (2009/147/EC) compels member states to classify PAs according to the presence of particular bird species, especially migratory species. Member states are required to ensure that birds in PAs are not significantly impacted by disturbance, pollution or habitat degradation. However, developments beyond PA boundaries can also impact the populations supported within PAs, through degradation of sites used by individuals that cross PA boundaries. Incorporating knowledge of individual movements across PA boundaries into assessments of development impacts is therefore urgently needed.

Information on movements of individual birds generated by ringing or electronic tracking (Anderson & Green, 2009; López-López, 2016), together with the development of analytical methods such as network analysis (Jacoby & Freeman, 2016), provides a framework for addressing this issue. Network analysis is the system-level study of connections (Proulx, Promislow, & Phillips, 2005), providing varied, versatile techniques to study ecological connectivity in a conservation context (Rayfield, Fortin, & Fall, 2011). A network is simply a collection of objects, dubbed *nodes*, linked by connections known as *edges*, which may have varying directions or strengths. Network analysis can describe an interconnected ecological system as a whole and quantify the contributions of individual components to overall connectivity (Table 1). Network metrics can also be used to compare connectivity of different networks, based either on empirical data or employing simulated networks to represent real or hypothetical scenarios of the potential consequences of environmental changes (e.g. Urban & Keitt, 2001).

Despite being powerful and flexible, network analysis is used more rarely by conservation practitioners than by academics (Zetterberg, Mörtberg, & Balfors, 2010). This may be because academic studies of ecological connectivity often take place at landscape- or regional-scales, focusing on general environmental improvement potential. Practitioners, however, frequently work at administrative scales smaller than, and independent of, the ecological functions they are tasked with protecting, and typically focus on minimizing and mitigating impacts from specific instances of anthropogenic habitat degradation (Bergsten & Zetterberg, 2013).

To increase their applicability, network analysis tools can be re-framed to better align with the scale and goals of conservation practice (Table 2). Designation of PAs, and Environmental Impact Assessments (EIAs), both typically use count data to assess the proportion of population(s) likely to be protected/impacted (Table 2: Aspect 1). However, connectivity of sites across PA boundaries has a series of implications for improving understanding of the functional role of PAs in species protection (Table 2; Protection Footprint), and for EIAs of developments straddling or occurring beyond PA boundaries (Table 2; Impact Footprint). For instance, movement data can reveal the range of sites used by individuals from a PA, and thus the susceptibility of those individuals to a localized impact, or conversely the range of sites used by individuals impacted by a local development (Table 2: Aspect 2). Network analyses can reveal which sites are most important to population-level connectivity, or the impact on connectivity of losing one or more sites (Table 2: Aspect 3). Together, these three aspects can be used to calculate the ‘impact footprint’: how many individuals use the impacted area, and how their movements connect it with neighboring sites (inside or outside the PA). The overlap of this ‘impact footprint’ with a PA is thus the severity of impact on the PA as mediated by ecological connectivity. Crucially, this impact footprint does not simply equal the spatial extent of the impact itself, but also encompasses all additional areas used by impacted individuals. Thus, by representing movements between sites in a network, practitioners can gain a more accurate picture of how the effects of a localized impact or protection may be felt at connected sites (Fig. 1). This information can then be used to determine whether populations or habitats are impacted or (adequately) protected, and thus inform policy application and development (Table 2: Aspect 4).

Table 1 Network metrics, their typical applications and ecological interpretations of high scores

Metric	Structure	Application	Interpretation
Degree	Number of other sites to which the focal site has a direct connection	Represents (topologically) local connectivity	Frequently-used hubs in the network (Fortuna *et al.*, 2009)
Betweenness (centrality)	Proportion of shortest paths through the network, from each site to every other site, that passes through the focal site	Role as intermediaries between disparate components of the network	Sites functioning as stepping-stones or bottlenecks (Lookingbill *et al.*, 2010)
Clustering	Probability that two (topologically) adjacent sites are connected	Network’s propensity to form subgroups (de Lima, Corso, & Cardoso, 2015)	Existence of subgroups of highly interconnected sites
Centralization	Extent to which centrality of most central site exceeds centrality of all other points, expressed as ratio of that excess to its theoretical maximum (Freeman, 1979)	Tendency of a single point to be more central than all other points in the network	Overall strength of a network-wide ‘bottleneck’ effect
Edge Density	Proportion of potential connections that are actually observed (or, the probability that any pair of sites is connected)	A measure of the overall interconnectedness of the network (Newman, 2010)	Individuals are moving between more sites across the network

Table 2 Protection-focused and impact-focused applications of network analysis to conservation problems

Aspect	(a) Protection footprint	(b) Impact footprint	Data/ analysis
1. Population	What % of population is protected?	What % of population is impacted?	Counts, resightings
2. Area	What is the wider area used by the protected population?	What is the wider area used by the impacted population?	Movement
3. Connectivity	Which sites contribute most to population connectivity?	How does impact affect population connectivity?	Network
4. Policy	Are populations/ habitats protected?	Are populations/ habitats impacted?	Review

For four key aspects of PA function (1. use by a population of interest; 2. coverage of the area used by that population; 3. connectivity with the wider landscape used by that population; and 4. contribution to population protection), network analysis can inform a series of questions to interrogate (a) protection by, or (b) impact of developments on, the PA and its populations, requiring differing data and analytical approaches.

To illustrate these concepts, we apply this framework to a current example of a proposed infrastructure development adjacent to (and slightly overlapping) a PA that covers a highly heterogeneous landscape (Alves & Dias, 2020). The Tagus estuary is Portugal's largest wetland and the country's most important site for many waterbird species (Alves, 2020). Part of the estuary is designated under the EU Birds Directive as a Special Protection Area (SPA; Alves, 2020); however, the SPA excludes several of the estuary's high-tide roosts, which often lack legal protection and are vulnerable to development, erosion and other threats (Catry *et al.*, 2011).

Eclipsing this shortcoming, however, are plans recently approved by the Portuguese Environment Agency to construct an international airport in the heart of this estuary, on a site overlapping part of the PA (Alves, 2020; Alves & Dias, 2020). The EIA conducted for the development considers the main threat of this development to bird conservation to be noise disturbance from aeroplanes, with one takeoff or landing every 2.5 min (PAO, 2019; Catry *et al.*, 2021), flying at low altitude (<200 m) over the SPA (PAO, 2019; Alves, 2020), and the consequent alterations in behavior, from alarm-calling to taking flight and leaving the disturbed area (Komenda-Zehnder, Cevallos, & Bruderer, 2003; Wright, Goodman, & Cameron, 2010; van der Kolk *et al.*, 2020a).

Overflight of large aircraft can cause birds to take flight, and substantial increases in shorebird daily energy expenditure when exposed to such aircraft disturbance have been recorded, even when the airport has been operational for decades (van der Kolk *et al.*, 2020b). Airport-related disturbance close to wetlands has also been shown to influence the spatiotemporal structure of their waterbird communities (Farinós Celdrán & Robledano Aymerich, 2010). Movement of animals, including birds, is known to be disrupted by disturbances arising from human activities (Doherty, Hays, & Driscoll, 2021). Consequently, many authors emphasize the need to limit the effects of anthropogenic noise in PAs (Barber, Crooks, & Fristrup, 2010; Herrera-Montes, 2018; Alquezar & Macedo, 2019).

The predicted impact of the Tagus airport development varies depending on the threshold of noise sensitivity assumed, with louder noise occurring over a smaller area. Although the EIA's reference for waterbird noise responses (Wright, Goodman, & Cameron, 2010) reported altered behaviors above 50 dB(A), the EIA itself only considers relevant areas impacted by over 65 dB(A) (the level at which Wright, Goodman, & Cameron, 2010 report 50% of birds showing altered behavior) and limited to areas within the PA (Alves, 2020). Crucially, individual movements within or to/from the PA were not considered. For species that regularly use sites inside and outside the PA or the noise-impacted zone, where such artificial limits lie is irrelevant (Barry & Suliman, 2022). Ignoring such impacts risks adversely affecting the integrity of the PA.

In order to demonstrate the applicability of this proposed framework, we use network analysis of individual movements of a conservation-priority species, the Black-tailed Godwit (*Limosa limosa*; hereafter: godwit) to assess the protection footprint of the Tagus estuary SPA and the impact footprint of the proposed airport. Specifically, we quantify (a) the proportion of the local godwit population protected by the PA during the year, and its overlap with the area to be impacted by development, and (b) the wider areas used by birds from the PA, and birds from the impacted area. Employing network analysis, we then assess which sites contribute most to connectivity, and how the predicted development impact might diminish connectivity.

Materials and methods

Data

For one of the species for which the Tagus estuary SPA was designated, the Black-tailed Godwit, life-long range-wide monitoring of marked individuals provides an ideal opportunity to capitalize on existing data as a case study. Birds are caught within the breeding (Iceland) and non-breeding ranges (west Europe), and marked with unique combinations of colored leg-rings (Gunnarsson *et al.*, 2005). All handling of animals followed the legislation and ethics guidelines in place in the relevant jurisdiction. Marked individuals are reported by 2000+ observers across Europe, providing georeferenced records of thousands of individuals throughout their lifespan and migratory range (Alves *et al.*, 2012, 2013; Gill et al., 2014; Gill, Alves, & Gunnarsson, 2019).

We collated data from individually-marked godwits marked in three locations: breeding in Iceland, stopover in the Wash,

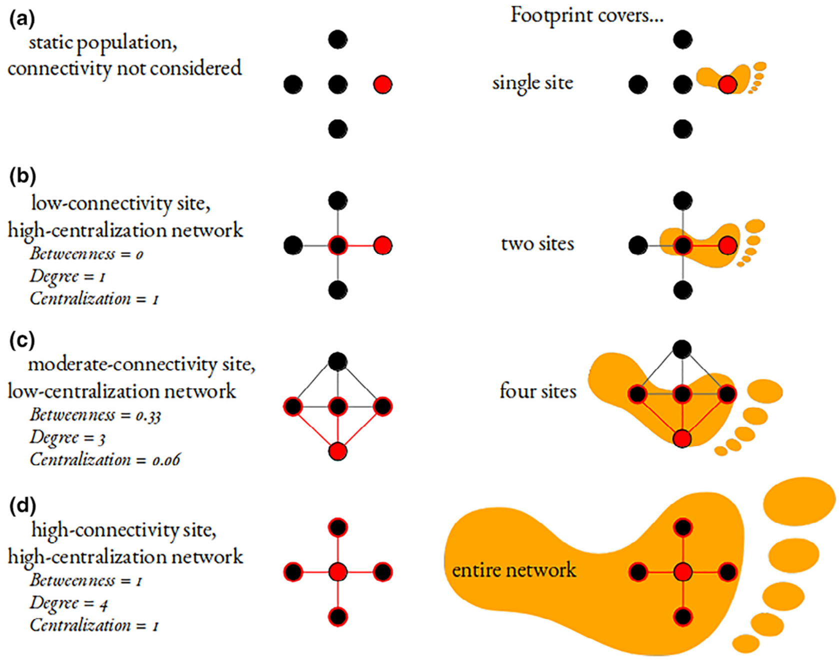

Figure 1 The size of an impact/protection footprint depends on both the connectivity of impacted sites and the configuration of the entire network. Environmental Impact Assessments typically assume (a) a static population, ignoring connectivity: in such cases the footprint only covers the site(s) directly impacted (red circles). When individual movements are also considered, the size of the footprint may increase, encompassing also any site(s) to which individuals move from the impacted area (black circles with red outlines; (b–d). A network with dense connections, such as (c), will typically result in a greater footprint than a sparsely connected network (b). Similarly, an impact on a central site (d) results in a larger footprint than an impact on a peripheral site (b). For scenarios (b–d) we report the normalized betweenness and degree of the impacted site, and centralization of this simple network (see Table 1 for more information on metrics).

UK, or wintering in the Tagus estuary (Appendix S1). Individuals with ≥1 observation in the Tagus estuary between 1st January 2000 and 1st July 2020 were included. In the Tagus estuary, observations were recorded at 30 sites, each comprising a distinct area of contiguous habitat used by godwits (Appendix S2). All 30 sites used by godwits are visited at least once during early and late winter (see below), and more frequently since October 2006, by volunteer observers to record marked individuals (Alves *et al*., 2013). To reduce the potential risk of observation error in recording of individual locations, only sites on which individuals were recorded at least twice during their lifetime were assigned to those individuals (Tucker et al., 2019). Within years, marked godwits had a mean (±SE) of 3.3 (±0.1) sightings in the Tagus, separated by 15.9 (±0.4) days.

To assess site-level noise-exposure, we used the projected limits of noise levels across the estuary published in the EIA as 55 and 65 dB(a) isophones (Fig. 2; Appendix S2), derived from calculations for passenger-jet takeoff and landing (PAO, 2019). Throughout this study we compared these two possible thresholds of noise disturbance, 65 and 55 dB.

We quantified the use of unprotected sites by the protected godwit population by calculating the proportion of individuals recorded at sites in the SPA, and therefore subject to statutory protection (n = 13 sites), that were also recorded at sites outside the SPA (n = 17 sites; see Fig. 2). Similarly, the area used by the affected population was calculated by quantifying the proportion of birds using the noise-impacted sites which were also recorded within the SPA. The winter period was divided into 'early' (October to December) and 'late' (January to March), owing to the considerable use of rice fields during second part of these periods (Alves *et al*., 2010).

Site use and fidelity

Published estimates (mean ± SE) of godwit diurnal home ranges during the non-breeding season range from 13.4 ± 3.6 km^2 (foraging only; Jourdan *et al*., 2022) to 49.2 ± 22.3 km^2 (during migratory stopover; Santiago-Quesada *et al*., 2014), compared with the 320 km^2 extent of the Tagus estuary itself (Alves, 2020). Each individual is therefore likely to use only a small portion of the whole estuary (see also Catry *et al*., 2012).

As site-fidelity can exacerbate mortality from site-loss (Burton *et al*., 2006), we quantified the total number of sites within the Tagus estuary used by each marked individual during the first n years of tracking, following Gill *et al*. (2019). The cumulative number of sites used per individual would only be expected to increase with increasing n years of tracking if individuals frequently change sites over the course of their lifetimes (Gill *et al*., 2019).

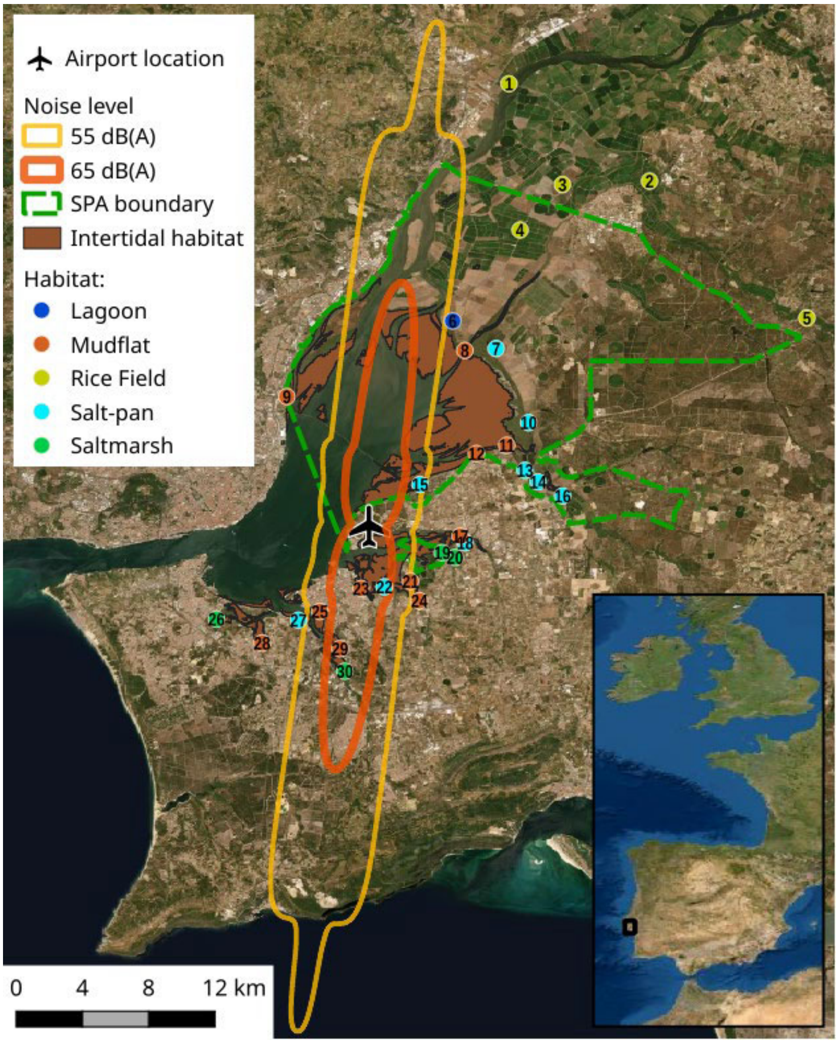

Figure 2 Spatial extent of two levels of noise predicted to occur over the Tagus estuary, including on the Tagus estuary Special Protection Area (SPA) and adjacent estuarine area, for the planned airport location (aircraft symbol) and the locations and habitats of the 30 sites (numbered circles; some points jittered to avoid overlapping) used by individually tracked godwits between 2000 and 2020. Inset: location of Tagus estuary in SW Europe. Key to sites: 1 Carregado; 2 Samora Correia; 3 Zé do Pinho; 4 Giganta; 5 Santo Estevão; 6 Evoa; 7 Vasa Sacos; 8 Ponta da Erva; 9 Trancão; 10 Val Frades; 11 Hortas; 12 Alcochete; 13 Enguias; 14 Atalaia; 15 Samouco; 16 Barroca d'Alba; 17 Montijo; 18 Lançada; 19 Sarilhos; 20 Espinhosa; 21 Gaio; 22 Alhos Vedros; 23 Baixa; 24 Moita; 25 Barreiro; 26 Corroios; 27 Seixal; 28 Arrentela; 29 Palhais; 30 Coina.

To assess the proportion of individual godwits protected and/or impacted, we independently calculated the number of marked individuals recorded using (1) the SPA and (2) the impacted area (see below), and divided by the total number of marked birds recorded across the Tagus estuary. Individuals recorded in both the protected and impacted areas contributed to both totals.

Network analysis

We generated a pre-development network by defining as connected any pair of sites between which an individual godwit had moved within a year. A movement was identified when an individual was recorded in two sites within the same winter (with the pre-migratory period of January–March included with the previous calendar year). Six sites with <10 confirmed observations or movements were excluded from the network analysis, as these sites are rarely used by godwits and network calculations are sensitive to the number of nodes, leaving a total of 24 sites included in the network analysis. Unique movements from all individuals were joined in a single unweighted network. We used the igraph R package (Csardi & Nepusz, 2006) in R 4.1.2 (R Core Team, 2022) for network analysis. Connections in this pre-development network allowed us to assess use of unprotected sites by godwits recorded within the SPA, and use of unimpacted sites by godwits recorded in the impacted area.

To determine which sites contribute most to population connectivity, we calculated each site's degree (number of connected sites) and betweenness (proportion of shortest paths through the site; Table 1). Both metrics were normalized by number of sites in the network to allow comparison between scenarios. We then compared degree and betweenness of sites impacted by each noise level with those of unimpacted sites, using permutational *t*-tests from the permuco R package (Frossard & Renaud, 2019) as the data were non-normal (Appendix S3), to determine whether the impact of development would disproportionately affect sites of greater importance to population connectivity.

To explore potential impacts of noise on connectivity, we simulated two constrained networks by excluding all sites impacted by noise above either 55 or 65 dB, representing scenarios where godwits avoid those sites (e.g. Farinós Celdrán & Robledano Aymerich, 2010). We compared the connectivity of sites (betweenness and degree; Table 1) between the three networks with permutational repeated-measures analysis of variance (ANOVA) from the permuco R package (Frossard & Renaud, 2019) as the data were non-normal (Appendix S3), with degree or betweenness as the response and the noise scenario as predictor. We restricted this analysis to sites appearing in all three networks, with site as the subject in the repeated-measures design. Post-hoc tests were conducted when the initial ANOVA was significant at the $p < 0.05$ level, using permutation-based paired *t*-tests from the pairwise.perm.t.test() function of the RVAideMemoire R package (Hervé, 2021), adjusting *P*-values with the Bonferroni correction.

We also calculated the network-level connectivity metrics (edge density, clustering and centralization; Table 1) of each scenario's network, in order to compare the networks' characteristics. To test the significance of these metrics, we compared the impact of removing the specific combination of impacted sites versus removing an equal number of randomly-selected sites, using Monte Carlo simulations to generate randomly-diminished networks. Specifically we used the delete_vertices() function from igraph (Csardi & Nepusz, 2006) to remove *n* randomly-selected nodes from the network by dropping the same number of sites, and then calculated the same network-level metrics for each of these 10 000 random networks to bootstrap probability distributions. We considered the scenario's connectivity metric to be significantly different from random if its value was outside the central 95% of the distributions thus generated.

Results

Site use and fidelity

The 693 individually-tracked godwits using the Tagus showed high inter-annual site-fidelity, with most individuals recorded at ≤6 of 30 sites even over 10+ years of tracking (Fig. 3): individuals are therefore restricted to a small subset of sites used consistently throughout their lives. Of these, 82.8% used sites inside the SPA and 67.7% used sites outside the SPA. Of individuals that used the SPA, 61.0% also used sites outside it. There was also seasonal variation in the protection footprint of the SPA, with only 26.3% of godwits recorded in the protected area during October–December, compared with 79.3% in January–March.

For the disturbance threshold used in the EIA (65 dB), 29.1% of godwits used ≥1 impacted sites. During the early winter period (October–December), the impact footprint of disturbance is predicted to cover 40.7% of individuals, whereas during the late winter (January–March), when godwits are most numerous, 22.6% of individuals would be affected. For the 55 dB disturbance threshold, impacts are even greater: 68.3% of individuals would be disturbed during early winter, and 37.8% during the later winter pre-migratory period.

Network analysis

We identified a total of 1619 individual movements (when an individual was recorded in two sites within the same winter) between 24 sites in the Tagus estuary. Of the 17 unprotected sites across the Tagus estuary network, 14 were used by at least one individual that also used the SPA (Fig. 2; all except sites 5, 9 and 28). There was also considerable interchange among protected sites (Fig. 4). Most (22 of 24) sites in the network were used by at least one individual recorded within the 55 dB impact zone, except for sites 5 and 8, the latter within the SPA (Fig. 4).

The SPA includes few of the sites most important for connectivity. Of the five sites with the greatest degree, three (17, 22, 27; Fig. 2; Appendix S4) were outside the SPA; two (15, 22) were within the 55 dB isophone and another (27) overlapped it by 43%. Each of these five was connected to at least 70% of the network (i.e. 17 other sites). The main 'stepping-stone' or 'bottleneck' site, with the highest betweenness (site 27; Fig. 2; Appendix S5), is outside the SPA but overlaps the 55 dB isophone by 36%.

Sites that would be disturbed by aircraft noise of 55 dB ($n = 7$) had significantly higher degree than unimpacted sites ($t = 2.2$, $n = 24$, $P = 0.04$), with connections to five more sites on average, but did not differ in betweenness ($t = 0.4$, $n = 24$, $P = 0.68$; Appendix S6). There was no significant difference in either metric for sites ($n = 3$) impacted by noise of 65 dB ($P > 0.05$).

After removing all sites that would be disturbed by aircraft noise above each threshold, effects on connectivity were detectable at both site and network levels (Fig. 5). Of the 24 sites in the pre-development network, 21 remained in the 65 dB network and only 17 in the 55 dB network (Fig. 5a). The impacted networks showed significantly reduced structuring, indicated by the clustering coefficient's decrease from 0.74 in the pre-development network to 0.59 in the 55 dB network (Fig. 5d; Appendix S7).

Sites in the diminished networks had fewer connections (Fig. 5b; Appendix S8), connecting to a median of 47.6% of remaining sites in the 65 dB network, and to only 35.3%

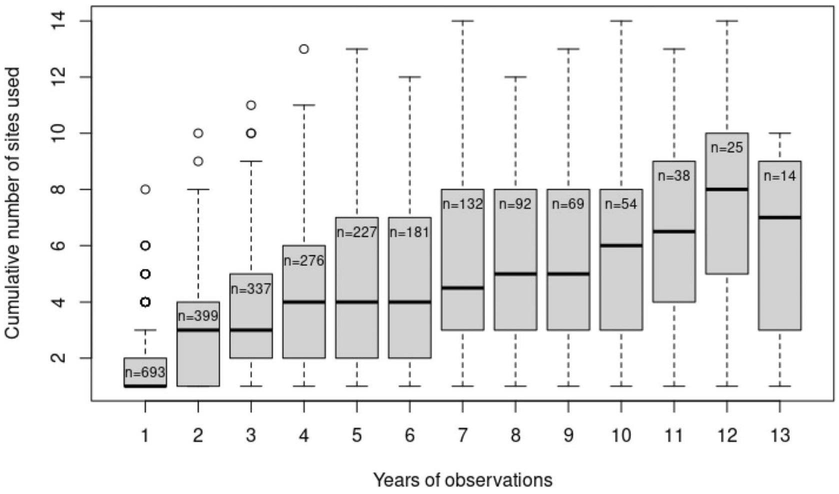

Figure 3 The total number of sites within the Tagus estuary at which individual godwits have ever been recorded during the total number of years for which each individual has been tracked. The sample size indicates the number of individuals tracked for the number of years indicated on the *x*-axis.

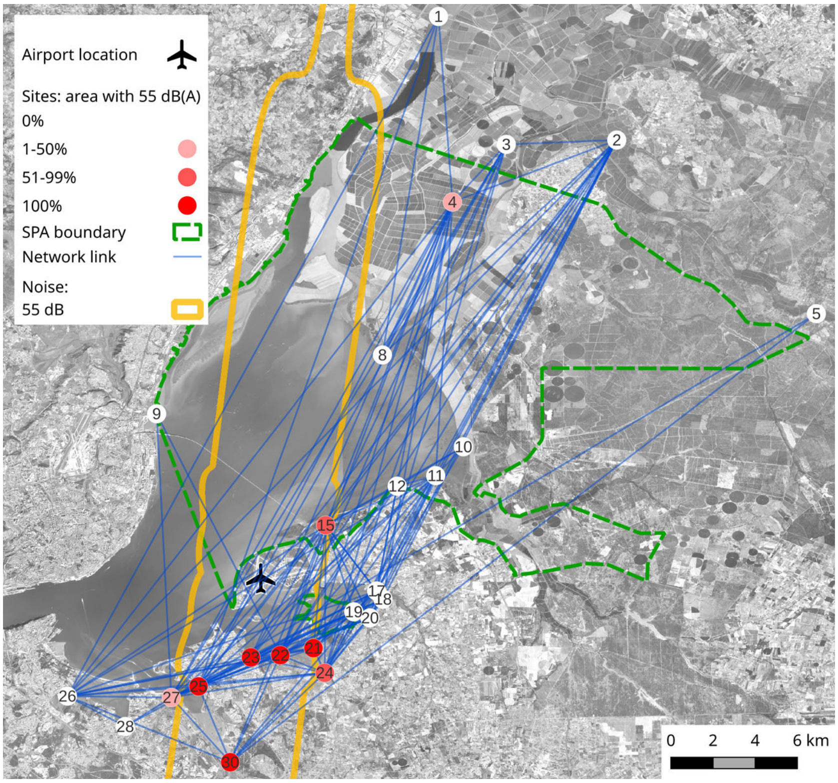

Figure 4 Connectivity among sites used (colored circles; numbers as Fig. 1) across the Tagus estuary. Sites are represented by dots indicating centroids, colored according to the % of the site area overlapping with the projected 55 dB noise isophone (yellow outline; see Appendix S2 for overlap calculations). Blue lines indicate connections between sites in the godwit network, representing movements by individual marked godwits within a winter season. The boundary of the Tagus estuary Special Protection Area is shown in green.

in the 55 dB network, compared with 52.1% pre-development. Pairwise testing showed that the 55 dB network differed significantly from the others in degree (Appendix S9). This significant decrease in connectivity (edge density) was also evident at the whole-network level: the 48.9% of possible connections observed in the pre-development network shrank to only 35.2% in the 55 dB network (Fig. 5e; Appendix S7).

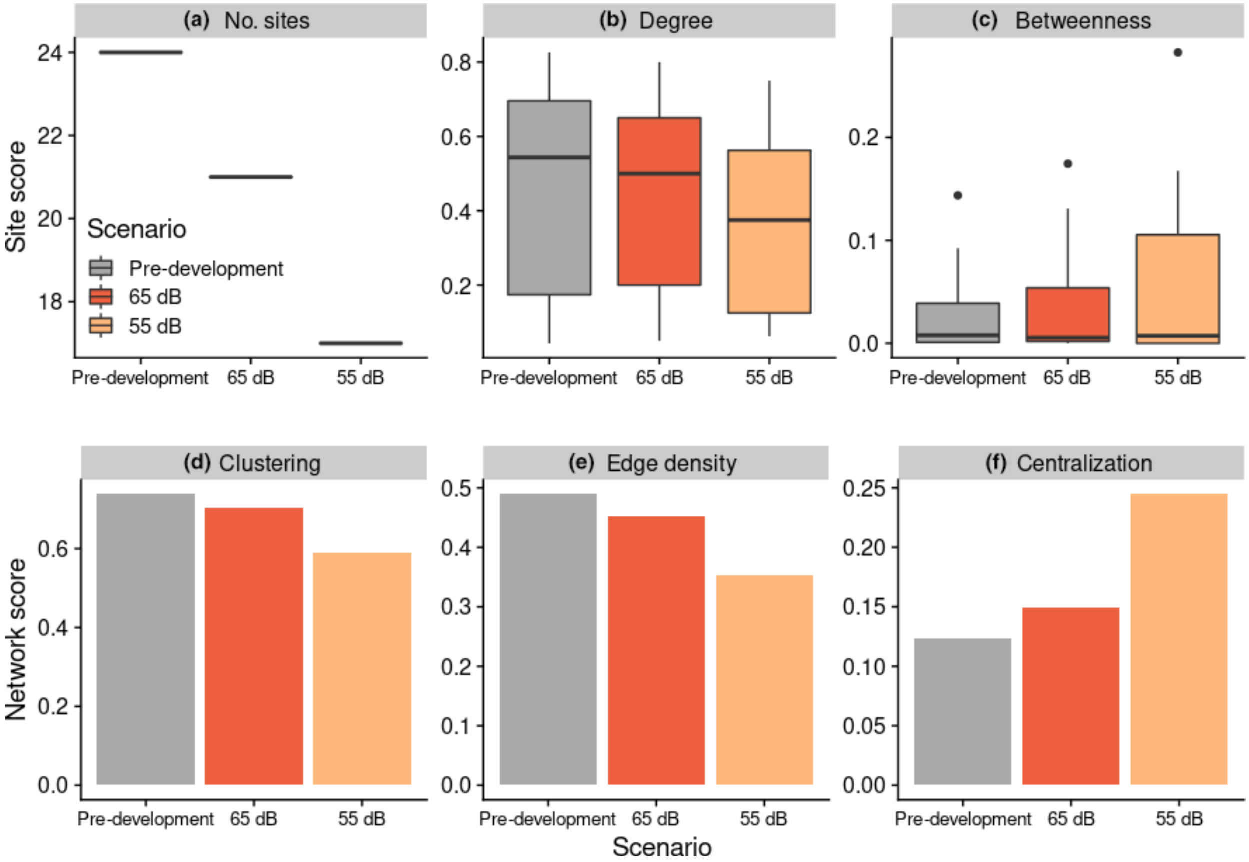

Figure 5 Differences between the characteristics of the current (pre-development) network of godwit movement across the Tagus estuary and the networks predicted to result from noise impact scenarios at 55 or 65 dB at the site-level (top row); (a) number of sites remaining in the network after removing sites above the disturbance threshold; (b) degree (proportion of connections to other sites in the network); and (c) betweenness (higher values = greater tendency to function as bottlenecks); and at whole-network level (bottom row); (d) clustering (higher values = sites more clustered into subgroups); (e) edge density (proportion of all possible connections between sites that are observed in the network); and (f) centralization (strength of a network-wide 'bottleneck' effect) (see Table 1 for further interpretations). Box-plots boxes show first quartile, median and third quartile; whiskers indicate range of data with outliers (>1.5*IQR) represented by points.

The impacted networks also showed stronger site-level bottleneck effects: maximum betweenness almost doubled between the pre-development (0.14) and 55 dB (0.28) networks, though the median differed little (Fig. 5c; Appendix S8). Pairwise testing showed that the three networks all differed significantly from the others in betweenness (Appendix S9). However, there was no significant change in the network-wide centralization index (Fig. 5f; Appendix S7).

Discussion

Protected Areas are a critically important conservation tool to protect populations, especially as ranges shift in response to climate change (Gaget *et al.*, 2021). To secure the integrity of PAs and the populations they support, we need to be able to accurately assess the impacts of developments inside and outside PA boundaries. Animal-tracking data offer exciting and feasible opportunities to assess PAs' contributions to protecting populations of mobile species and the potential for adverse effects of external developments on PA integrity.

Here, we used network analysis of locations of marked individuals to assess the protection footprint (Table 2) of the Tagus estuary SPA as it pertains to godwits, and the impact footprint (Table 2) of a proposed airport development adjacent to, and slightly overlapping, the SPA. We found that, while protection from the Tagus estuary SPA covers 82.8% of the godwit population for at least some portion of the year, frequent trans-boundary movements mean that 61.0% of those individuals use unprotected sites as well. In fact, 14 of 16 unprotected sites were found to support birds that also use the SPA. We also found that the majority of the most important sites for connectivity were outside the protected area. Taken together, these results show that the surrounding, unprotected landscape plays an integral role in supporting the SPA's godwits, especially during October–December.

Frequent disturbance by aircraft is known to have fitness costs for waders by increasing their energy expenditure (van der Kolk *et al*., 2020a; van der Kolk *et al*., 2020b), and may cause permanent avoidance of habitat if chronic (Catry *et al*., 2021) with long-term consequences for site occupancy (Farinós Celdrán & Robledano Aymerich, 2010). The Tagus godwits' frequent trans-boundary movements mean that 44.6% of the SPA's godwit population would be exposed to noise disturbance from the proposed airport, and 68.3% of individuals overall. This compares with estimates of 0.46–5.5% in the airport's EIA (Appendix S10). One reason for this discrepancy is our consideration of all impacts above 55 dB(A), as suggested by Wright, Goodman, & Cameron (2010), whereas the EIA restricts consideration to disturbance over 65 dB(A), the level at which Wright, Goodman, & Cameron (2010) reported up to 50% of birds showing altered behavior. Even the threshold of 55 dB(A) should be considered conservative, as Wright et al.'s study was based on three seconds of irruptive noise alone, without the accompanying visual stimulus of an aircraft which also causes disturbance (van der Kolk *et al*., 2020a). Furthermore, the proposed frequency of disturbance events (on average one per 2.5 min during operating hours; PAO, 2019) suggests that disturbance in the Tagus would effectively be chronic, potentially leading to causing permanent abandonment of disturbed areas (Catry *et al*., 2021).

We found that many of the sites most important to connectivity in the estuary, which include both feeding and roosting areas, would receive at least 55 dB of aircraft noise, and that threatened sites are connected to five more sites on average than unthreatened sites. Simulating avoidance of those sites by godwits revealed significantly reduced connectivity across the estuary-wide movement network, as well as increasing the relative importance of the remaining sites, many of which currently lack statutory protection. Indeed, loss of the potentially-impacted sites is predicted to have a larger effect on the network than removing the same number of sites at random, suggesting that an airport in the proposed location would alter connectivity by reducing the amount of available habitat. The high level of site-fidelity of individual birds would likely exacerbate the mortality from site loss (Burton *et al*., 2006). It therefore seems likely that the proposed development would lead to a decrease in the size of the godwit population in the Tagus estuary SPA, through death and/or relocation of individuals that depend on the impacted area (especially during early winter), as well as increasing disturbance and physiological stress, and reducing habitat availability, of those that remain.

While the resighting data we use are more recent and spatially extensive than the count data used in the EIA to evaluate impacts on birds owing to noise, and includes the early half of the winter period, some limitations remain. Other species may show different patterns of site-fidelity or movement, which could be confirmed using color-ring or electronic tracking data. While godwits tend to use smaller foraging areas at night, the sites used may be distinct from daytime areas (Jourdan *et al*., 2022), but obtaining color-ring observations in the darkness is impossible. However, the airport would continue to operate during darkness, and any reduction in flight activity at night would not reflect the tidal cycles that determine when intertidal feeding areas are available for foraging birds. There is therefore unlikely to be much opportunity for compensatory nocturnal feeding in disturbed areas.

Site-use networks show how PAs and the wider landscape operate as an integral unit. Impacts on individuals using the PA, including those also using unprotected sites outside the PA boundary, adversely affect the integrity of the PA itself. Thus, network analysis of animal movement enables practitioners to assess PAs' effectiveness in protecting populations of interest ("protection footprint"; Table 2), and to refine estimates of localized impacts within the wider context given by ecological connectivity ("impact footprint"; Table 2).

Network analysis is rarely incorporated into EIAs (Bergsten & Zetterberg, 2013). However, one example of application in local planning policy is the Solent Wader and Brent Goose Strategy, a collaboration between NGOs and statutory entities centered on the Solent estuaries, UK (Whitfield, 2020). Using systematic observations of flock movements, sites are scored on degree and betweenness, with the most important sites for connectivity prioritized for protection to enhance the protection footprint of adjacent offshore PAs. At the international scale, network analysis can also be applied to longer-distance movements like migration. Iwamura *et al*. (2013) found the impact footprint of habitat loss on migrating shorebirds was mediated by network topology, with impacts exacerbated by loss of areas that function as bottlenecks to movement, and Xiao *et al*. (2021) demonstrated larger protection footprints if conservation resources are targeted at sites that play a key role in connectivity. This is particularly relevant for large-scale networks of PAs, like the EU's Natura 2000 network.

Practitioners may wish to consider using network analysis in situations where movement of individuals could make the impact of a development broader than suggested by counts alone (see Table 2). Network analyses can improve understanding of systems that function ecologically as a whole via connectivity but are heterogeneous in management, habitat type or other factors. In addition to incorporating network analyses into EIAs for development proposals, applications could include identifying appropriate areas for protection, determining appropriate types and scales of compensatory habitat creation following development and contributing to Biodiversity Net Gain assessments (zu Ermgassen *et al*., 2021). Movement networks can be defined for any set of geographical units connected by recorded individual movements, which could include direct observations of movements (e.g. Whitfield, 2020), mark-recapture data (e.g. de Lima, Corso, & Cardoso, 2015; this study) or records from electronic tracking (e.g. Fortuna *et al*., 2009; Choi *et al*., 2019), the latter of which is increasingly available for a broad range of species (Jetz *et al*., 2022). The required spatiotemporal resolution of movement data could range from local, for example a single PA and its habitats, to international, for example, the flyway of a migratory bird population, depending on the scale of relevant issues, such as PA area, organismal home range and the area of the potential impact. In all cases, practitioners should aim to include data from as large and unbiased a sample of individuals as possible to be representative of the population over the entire range and period of interest (Vickers, Franco, & Gilroy, 2021). Existing monitoring data may also help to calculate relevant metrics such as levels and scales of site-fidelity, home-range size and repeatability of movements. Accessible introductory guides are available to conduct network analysis using standard statistical software, for example Luke (2015) for R.

Individuals frequently avoid sites impacted by factors which can be difficult to detect directly via remote methods, such as high risks of disturbance or persecution (Geldmann *et al*., 2021). Quantifying how sites are used and connected by individuals, however, is now possible in real-time and high-resolution, thanks to technological developments in animal tracking (Katzner & Arlettaz, 2020; Geldmann *et al*., 2021; Jetz *et al*., 2022). Tracking individuals thus offers real-time information regarding impacts on PAs' integrity and connectivity, as well as the potential to identify key sites, and groups of sites, for protection.

Portugal and 70 other states have recently committed to protecting 30% of the planet's land and ocean by 2030 (HAC, 2022). Network analysis of data on animal positions can make a valuable contribution to this laudable goal in three ways. Firstly, by ensuring that PAs encompass a useful proportion of the area used by target species (Choi *et al*., 2019; Bhola *et al*., 2021). Secondly, by guiding improved connectivity between existing PAs (Hilty *et al*., 2020). Thirdly, by enabling accurate assessment of the scale of impacts from developments in or near to PAs, so that such impacts can be appropriately mitigated or prohibited (Amano *et al*., 2018).

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Author contributions

JN, JAA and JAG conceived the ideas and designed methodology; JAA, BD, PMP and JAG managed the data; JN analyzed the data; JN, JAA and JAG led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility statement

All data and code necessary for the analyses herein are provided at dx.doi.org/10.6084/m9.figshare.19170176.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Numbers of individual Black-tailed Godwits included in this study, and numbers of observations in the Tagus Estuary, from each data source (colour-ringing location) between 2000 and 2020

Appendix S2. Spatial data and calculations.

Appendix S3. Permutation tests

Appendix S4. Site degree (number of connected sites) for pre-development scenario and two thresholds for behavioural response to from the proposed airport development, 65 and 55 dB. A hyphen (–) indicates that the site in question was removed from that scenario (i.e. would be unused). Protection column indicates maximum level of statutory protection for the site. Site number refers to Figure 1.

Appendix S5. Site betweenness (proportion of shortest-paths through that site) for baseline scenario and two thresholds for behavioural response to from the proposed airport development, 65 and 55 dB. Protection column indicates maximum level of statutory protection for the site. A hyphen (–) indicates that the site in question was removed from that scenario (i.e. would be unused). Site number refers to Figure 1.

Appendix S6. Variation in degree and centrality between sites affected by noise disturbance in excess of 55 dB and all other sites. Sites affected by noise disturbance have significantly higher degree than unaffected sites (permutational $t = 2.3$, $P = 0.03$), but no significant difference is apparent in betweenness.

Appendix S7. Bootstrapped distributions of network metrics, obtained by dropping an equal number of randomly-selected sites from the pre-development network. Grey bars are a histogram of 10 000 replicates; dotted grey lines show the 95% confidence intervals (2.5 and 97.5% percentiles) and the solid coloured vertical line shows the observed value for the reduced network representing each noise scenario (see also Figure 6).

Appendix S8. Permutational repeated-measures ANOVA models testing the variation of sites' degree or betweenness in networks from three scenarios (pre-development, 65 and 55 dB). Only the 18 sites retained in all three networks were compared. We report the degrees of freedom, *F* statistic and permutational *P*-value. Significant *P*-values are in bold.

Appendix S9. Post-hoc testing used permutational paired t-tests to compare the results from each scenario: pre-development, 65 and 55 dB. We report the Bonferroni-adjusted permutational *P*-values. Significant *P*-values are in bold.

Appendix S10. Comparison with Black-tailed Godwit assessment in EIA.

Appendix S11. Literature cited in Supporting Information.