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Functional connectivity network between terrestrial and aquatic habitats by a generalist waterbird, and implications for biovectoring

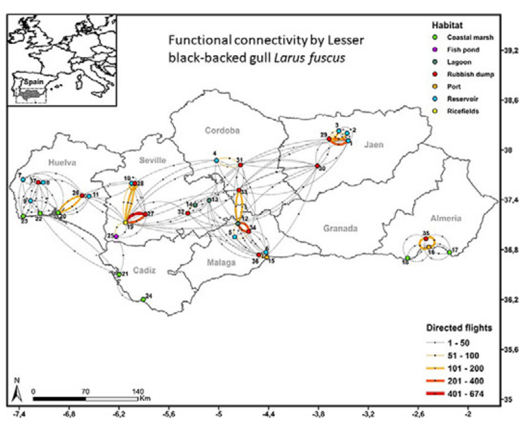
Víctor Martín-Vélez [a,*], B. Mohring [a], C.H.A. van Leeuwen [b], J. Shamoun-Baranes [c], C.B. Thaxter [d], J.M. Baert [e,f], C.J. Camphuysen [g,h], A.J. Green [a]

[a] Department of Wetland Ecology, Estación Biológica de Doñana EBD-CSIC, Américo Vespucio 26, 41092 Sevilla, Spain
[b] Department of Aquatic Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Droevendaalsesteeg 10, 6708 PB Wageningen, the Netherlands
[c] Theoretical and Computational Ecology, Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, PO Box 94240, 1090 GE Amsterdam, the Netherlands
[d] British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK
[e] Terrestrial Ecology Unit (TEREC), Ghent University, K.L. Ledeganckstraat 35, 9000 Ghent, Belgium
[f] Behavioural Ecology and Ecophysiology group, University of Antwerp, Universiteitsplein 1, 2610 Antwerp, Belgium
[g] COS Department, Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, the Netherlands
[h] Utrecht University, the Netherlands

HIGHLIGHTS

- The functional connectivity network of wintering gulls links seven habitat types.
- Ricefields acted as the central node in the network, but a third of nodes are landfills.
- Landfills are highly connected with wetlands, facilitating biovectoring of nutrients, contaminants and pathogens.
- Connectivity was low between nodes separated by >60 km.
- The network contains ten functional units (modules), each with rubbish dumps and nearby wetlands.

GRAPHICAL ABSTRACT



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ABSTRACT

Birds are vectors of dispersal of propagules of plants and other organisms including pathogens, as well as nutrients and contaminants. Thus, through their movements they create functional connectivity between habitat patches. Most studies on connectivity provided by animals to date have focused on movements within similar habitat types. However, some waterbirds regularly switch between terrestrial, coastal and freshwater habitats throughout their daily routines. Lesser black-backed gulls that overwinter in Andalusia use different habitat types for roosting and foraging. In order to reveal their potential role in biovectoring among habitats, we created an inter-habitat connectivity network based on GPS tracking data. We applied connectivity measures by considering frequently visited sites as nodes, and flights as links, to determine the strength of connections in the network between habitats, and identify functional units where connections are more likely to happen. We acquired data for 42 tagged individuals (from five breeding colonies), and identified 5676 direct flights that connected 37 nodes. These 37 sites were classified into seven habitat types: reservoirs, natural lakes, ports, coastal

* Corresponding author.
E-mail address: victormartin_velez@hotmail.com (V. Martín-Vélez).

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marshes, fish ponds, rubbish dumps and ricefields. The Doñana ricefields acted as the central node in the network based on centrality measures. Furthermore, during the first half of winter when rice was harvested, ricefields were the most important habitat type in terms of total time spent. Overall, 90% of all direct flights between nodes were between rubbish dumps (for foraging) and roosts in other habitats, thereby connecting terrestrial and various wetland habitats. The strength of connections decreased between nodes as the distance between them increased, and was concentrated within ten independent spatial and functional units, especially between December and February. The pivotal role for ricefields and rubbish dumps in the network, and their high connectivity with aquatic habitats in general, have important implications for biovectoring into their surroundings.

1. Introduction

Birds can efficiently exploit spatial and temporal variation in their environment to take advantage of seasonal peaks in food availability (Alerstam et al., 2003), track suitable climatic variation (Tingley et al., 2009) or reduce intra- or interspecific competition (Somveille et al., 2015). As such, birds can act as biological links among a wide range of habitat patches in ecosystems (Buelow and Sheaves, 2015), which can facilitate functional connectivity – defined here as the degree of movement or flow of organisms and their ecological functions through the landscape matrix (Taylor et al., 1993). Examples of functional connectivity are the dispersal of propagules of sessile organisms (Green and Figuerola, 2005; Lovas-Kiss et al., 2018), nutrients (which can lead to guanotrophication, Dessborn et al., 2016, González-Bergonzoni et al., 2017; Hahn et al., 2007, 2008), pathogens (Bauer and Hoye, 2014) or contaminants (Blais et al., 2007). These biovector processes occur mainly through the deposition of faeces and regurgitated pellets (Martín-Vélez et al., 2019). Connectivity is particularly high when different sites are used on a regular basis for different behaviours, creating a "functional unit" for the birds, e.g. when different wetlands are used by waterbirds for feeding and roosting (Guillemain et al., 2010).

Many studies on the functional contribution of birds to ecosystem connectivity have focused on terrestrial habitats, such as fragmented forests (Doerr et al., 2011; Mueller et al., 2014). Other studies have examined connectivity by waterbirds between wetlands or connectivity among different biomes (Haig et al., 1998; Merken et al., 2015; Obernuefemann et al., 2013). However, birds also frequently move between terrestrial and aquatic systems, which sometimes are separated by great distances (González-Bergonzoni et al., 2017; Soininen et al., 2015; Viana et al., 2016). For instance, many waterbirds consume terrestrial resources during the daytime but roost in aquatic environments at night. Geese feed on agricultural lands and move to nearby freshwater ecosystems to roost, thereby loading external nutrients into aquatic systems (Dessborn et al., 2016; Unckless and Makarewicz, 2007). Gulls also feed opportunistically in a wide range of terrestrial habitats while roosting in wetland habitats (Martín-Vélez et al., 2019; Winton and River, 2017) enabling functional connectivity between terrestrial and aquatic habitats (Hessen et al., 2017). In recent years, improvements in the quality of tracking data allow connectivity studies at high spatial or temporal scales (Morris, 2012). Such studies of functional connectivity would help us to understand the effects of waterbird movements on wetland functioning (Green and Elmberg, 2014), and be useful tools for the development of management plans (Amezaga et al., 2002; Si et al., 2018). Nevertheless, there is still little information regarding the role of waterbirds as functional connectors among different habitats. In this study, we aim to create an inter-habitat connectivity network based on GPS tracking data.

Gulls (Laridae) are a group of waterbirds known for movements between terrestrial, freshwater and marine habitats. The Lesser black-backed gull (LBBG) *Larus fuscus* has a European wintering population of over half a million birds (Hagemeijer and Blair, 1997; Wetlands International, 2019) and has become an abundant wintering waterbird on inland water bodies. This species is a generalist omnivore that uses a range of terrestrial, freshwater and marine habitats (Camphuysen et al., 2015; Tyson et al., 2015). Global Positioning System satellite tracking has shown that individuals from breeding populations in Belgium, the United Kingdom and the Netherlands spend part of the non-breeding season in Andalusia in southern Spain (Baert et al., 2018; Klaassen et al., 2011; Shamoun-Baranes et al., 2017; Thaxter et al., 2019). Given their great movement capacity, broad niche and habit of foraging and roosting in different locations, the LBBG is an excellent species for studying functional connectivity between different habitat patches.

In Andalusia, the LBBG exploits food in various habitats. Ricefields in the Doñana wetland complex are important for many waterbird species, including gulls, and provide abundant food during the harvest period, such as the alien red swamp crayfish *Procambarus clarkii* exposed during harvesting and tilling (Lovas-Kiss et al., 2018; Rendón et al., 2008; Toral and Figuerola, 2010). There are also numerous uncovered rubbish dumps (landfills) in open areas (Navarro et al., 2016). Rubbish dumps provide accessible food resources, which contain nutrients, contaminants and pathogens that can potentially be introduced by gulls into reservoirs, lakes and other environments used for roosting (Arnold et al., 2016; Duhem et al., 2005; Martín-Vélez et al., 2019; Winton and River, 2017). Coastal ports are also a feeding habitat, since they provide access to marine discards (Oro, 1996) and individuals that use these resources can potentially connect coastal and inland habitats. However, temporal changes in food availability in different habitats during the winter period may lead to movements of gulls around the network of sites across the Andalusian landscape. Changes in food availability and accessibility likely determine the decision to spend time in certain foraging habitats, or to move to new habitats with higher amount of food resources, influencing the functional connectivity. Because flight is relatively costly and birds should balance their energy expenditure with their energetic intake (Ydenberg, 1994), we can also expect the distance between foraging or roosting sites to be an important determinant of the level of functional connectivity within the network of sites.

The main aim of this study is to determine the extent to which gulls connect different habitat types, in order to understand their potential role as biovectors across terrestrial and aquatic habitats. We used a connectivity network approach based on direct flights derived from GPS data to explore the functional connectivity provided by LBBGs within Andalusia. Our specific objectives were: (1) identification of the main habitat types (and nodes) that make up the regional network, and the relative role of each habitat in maintaining functional connectivity, by quantifying how much time individually-tracked gulls spent in different habitat types, the strength of the different connections and centrality measures. (2) Study the strength of connectivity between terrestrial and wetland habitats, and between coastal and inland habitats. (3) Determine if distance has a negative effect on the degree of connectivity between sites, and identify functional units at a local scale through connectivity analyses. (4) Investigate the change in connectivity provided by gulls over the course of the winter season.

2. Material and methods

2.1. Study region

We studied flights of Lesser black-backed gull (LBBG) in the Spanish autonomous region of Andalusia. Andalusia holds 56% of the total surface area of natural wetlands in Spain (Consejería de Medio Ambiente, 2005) – including the Doñana wetland complex – and contains the majority of waterbirds wintering in Spain (del Moral, 2003). The Doñana wetland complex is the most important site in Spain for wintering waterbirds, and holds extensive natural marshes as well as ricefields, fish ponds and salt ponds (Green et al., 2018; Rendón et al., 2008). The area of ricefields has doubled since the 1960s, and is particularly important for LBBG (Ramo et al., 2013; Rendón et al., 2008). Elsewhere in Andalusia there are over 30 natural, closed-basin shallow lakes (known locally as "lagoons", Rodríguez-Rodríguez, 2007), and numerous large and small reservoirs constructed to supply agriculture and urban areas (Lehner et al., 2011).

2.2. Gull tracking data

The LBBG is a well-studied bird species in Western Europe. A number of ongoing studies have equipped adult LBBG with Global Positioning System (GPS) trackers between 2008 and 2018, using the UvA-BiTS tracking system (Shamoun-Baranes et al., 2017; Stienen et al., 2016; Thaxter et al., 2015). Details of the GPS tracking system can be found in Bouten et al. (2013) and examples of fieldwork and attachment methods can be found in Baert et al. (2018), Thaxter et al. (2019) and Van Donk et al. (2019). All tracking data is stored in a centralized database (http://www.uva-bits.nl; Bouten et al., 2013). Data is stored in GPS positions or fixes. Position accuracy with a stationary signal every 10 min was on average 30 m (Bouten et al., 2013).

From UvA-BiTS database, we first selected all GPS positions between latitudes 36.0–40.5° N and longitudes of 9.0–0.0° W that belong to the Andalusia region. We selected gull positions between October and March (the wintering period), which ensured that at least 20 different tagged individuals were present in any given month between October 2010 and March 2017 (i.e. seven winters). For our analysis, we used the following parameters recorded by the GPS trackers: date, time, latitude, longitude and instantaneous speed. We calculated additional variables from consecutive GPS positions: Harversine distance (spherical distance between geographic coordinates of GPS fixes), time difference between fixes, and trajectory speed (km/h as distance/time).

We filtered the dataset for quality by deleting any fix with ground speeds (either instantaneous or trajectory) exceeding 80 km/h, as this covers most recorded flight speeds for this species (Shamoun-Baranes et al., 2017). We filtered the database for gaps of >60 min between fixes, assuming these to be caused by e.g. battery depletion. We also deleted trajectories from gulls that were in transit on their migration towards Africa (see Klaassen et al., 2011; Thaxter et al., 2019). The resulting dataset included trajectories from 74 individuals belonging to five breeding colonies in North Europe (Walney, Skokholm, Zeebrugge, Texel and Orford Ness). Some individuals were present in Andalusia during several winters, making a total of 114 bird-winters (referred to as "bird-years" from here on).

2.3. Site selection

To create a connectivity network for the region of Andalusia, we first identified the 13 most important sites for LBBG according to wintering waterbird count data (data provided by Junta de Andalucía), these being the sites with a mean January (between 2010 and 2017) count of over 1000 birds. In addition, we used hotspots of GPS data to identify 24 other sites important for LBBGs, 17 of which were not covered by the waterbird censuses. Those hotspots showed any GPS activity and were considered as wetlands, rubbish dumps or ports (roost or foraging sites) according to CORINE Land Cover 2012 (Coordination of Information on the Environment, CLC; https://land.copernicus.eu/). Combining census information and hotspots from tracking data, we therefore identified the 37 most important sites within the study region, which we classified into seven main habitats to facilitate analysis: rubbish dumps (12), reservoirs (11), coastal marshes (7), lagoons/shallow lakes (3, two of which were complexes of several small lakes), ports (2), ricefields (1) and fish ponds (1) (Fig. 1, Table 1). We delimited the sites based on the polygons associated with CLC 2012 habitat types, and applied a 200-m buffer around the perimeter to account for gulls that may be resting around the site before departing. Spatial data processing was carried out using ArcMap 10.4. The 37 selected sites held 71.6% (410,623 out of 573,096 fixes) of all the GPS fixes available for the whole Andalusia region. The only fish pond site was Veta la Palma in Doñana Natural Park (Walton et al., 2015), the ricefields were also in the Doñana wetland complex (Rendón et al., 2008). The most important natural shallow lake was Fuente de Piedra (the largest natural lake in Andalusia; Batanero et al., 2017, Martín-Vélez et al., 2019).

2.4. Flight selection

We filtered the dataset to identify "direct flights" (i.e. without stopping) from one site to another. Although flight speeds are variable (Shamoun-Baranes et al., 2016), we considered direct flights to be represented by instantaneous or trajectory speed ≥ 10 km/h (after examining histogram of speeds for cut-offs). We defined a flight as the trajectory between two sites in which instantaneous or trajectory speed was ≥ 10 km/h, beginning and ending with a speed in each site < 10 km/h. This process excluded cases where a bird simply flew over a site. For the identification of direct flights, we also discarded trajectories with more than one fix with a ground speed lower than 10 km/h (either instantaneous speed or trajectory speed), as this implied a pause in between sites (Shamoun-Baranes et al., 2011; Klaassen et al., 2011). After this screening process we removed flights of more than one day (24 h), because retention times of content in the digestive system suggest such long flights would contribute little to biovectoring (Nogales et al., 2002). After this selection process, we had identified 5676 direct flights between the selected sites, performed by 42 tagged gull individuals (and 84 different bird-years).

2.5. Habitat use

We quantified habitat use as the percentage of time spent by tagged gulls in each habitat type, and site for each of six months (October–March), including the seven study winters, in order to identify seasonal patterns (objectives 1 and 4). We performed all data filtering and calculations in R (v.3.4.4. R Core Team, 2018).

2.6. Connectivity network

We considered each of the 37 sites within Andalusia as an independent "node", and considered direct flights between these nodes as "links" in the connectivity network. We calculated "betweenness" (objective 1) measures to identify central nodes in the network (Bastille-Rousseau et al., 2018) by making the links binary (connected/not connected). "Betweenness" is a centrality measure that quantifies the number of times a node acts as a bridge along the shortest path between two other nodes, and was calculated with the R package *igraph* (Csardi and Nepusz, 2006).

We then weighted the strength of each link between nodes by calculating the total number of direct flights (objective 1 and 2). We considered the links between nodes as directed or asymmetrical (i.e. for a given pair of nodes *ij,* the number of direct flights from node *i* to node *j* is different to the number of direct flights from node *j* to node *i*).

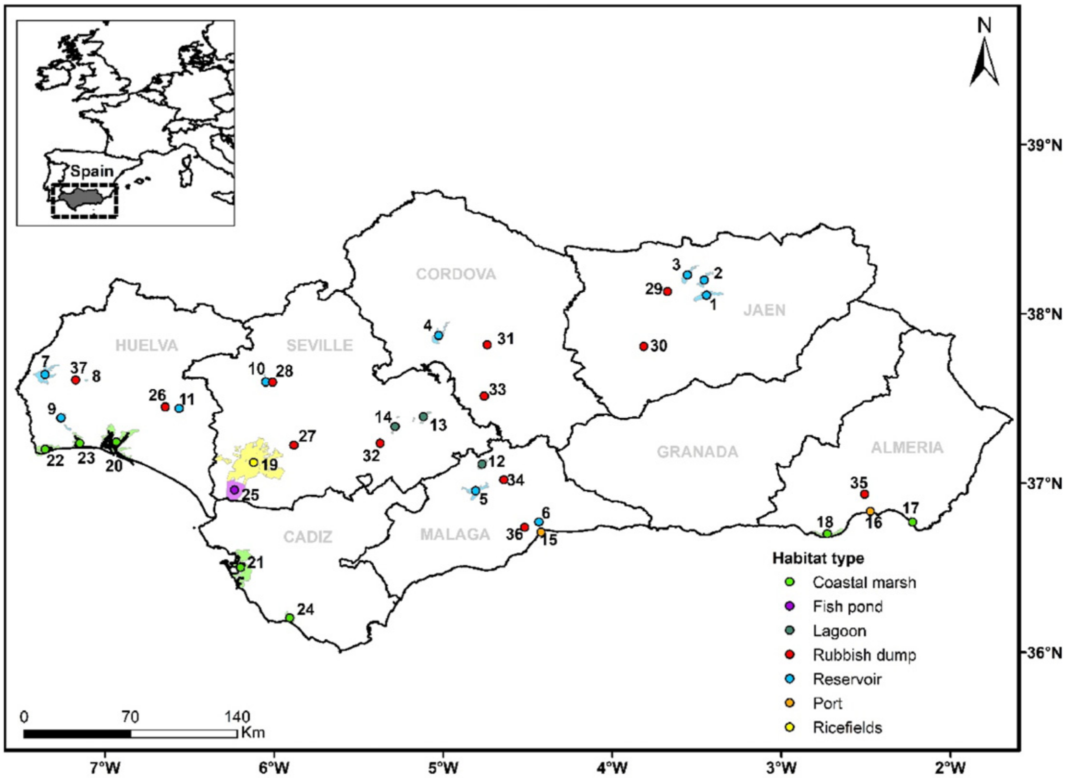

Fig. 1. Location of the 37 sites within Andalusia region in South Spain, classified into seven main habitat types.

We calculated distances between nodes using the Harversine formula, taking polygon centroids as a reference. In order to study whether distances between nodes could predict the number of direct flights in terms of connectivity, we used a Generalized Linear Model in which "number of direct flights" was the dependent variable and "distance" between sites and "number of gulls" were explanatory variables (objective 3). We fitted the model with a quasi-Poisson error distribution to account for overdispersion of the data and to normalize model residuals through *lme4* R package (Bates et al., 2014).

We identified the main "functional units" within our network (i.e. those sets of nodes which have high connectivity within a set, and low or no connectivity between sets) by applying the *cluster_infomap* function in *igraph* (Csardi and Nepusz, 2006), based on a probability of flow of random walks to detect structures in communities (Rosvall and Bergstrom, 2008). This function finds a community structure (in this case, it creates modules that we consider to be functional units) that minimizes the expected description length of the random walk trajectory. A random walk is generated that makes use of the network based on the probability (weight) of traversing a particular link (in this case weighted by the number of direct flights), and repeats the random trajectory generation ten times. We created a map for this directed and weighted connectivity network, including the ten resulting functional units in ArcMap 10.4 (objectives 1, 2 and 3). We split the connectivity network into six months (from October to March) and counted the number of flights within and between each functional unit. In this way, we could identify the temporal change in relative importance of each functional unit (objective 4).

3. Results

There was a total mean of 67,946 LBBG individuals counted in the 20 sites (54% of 37 sites) with midwinter census data available for Andalusia in January between 2010 and 2017 (Table 1). Those counts were dominated by two sites: Fuente de Piedra lake (FPL) with a mean of 18,690 gulls and Doñana ricefields (DR) with 10,800 gulls. These two sites also correspond to areas with a high relative time spent during the entire winter (12.08% and 43% respectively, Table 1). For the remaining 17 sites (10 dumps, 5 reservoirs and 2 ports) identified as GPS hotspots, no census data were available (Table 1). Sites with no census data accounted for 21.7% of the total relative time spent, including sites where a high proportion of total time was spent (e.g. 5.26% at Alcala de Guadaira Dump [AGD] and 5.61% at Linares Dump [LD], Table 1).

3.1. Habitat use

There was high seasonal variability in habitat use by the tagged gulls among the different months in winter (Fig. 2). Ricefields were the most important habitat during the first half of the winter, especially in October–November, when most gull activity in Andalusia was concentrated in this single, large site (Figs. 1 and 2). The time that gulls spent in ricefields decreased from December onwards, whereas time spent in other habitats such as dumps, reservoirs and lagoons increased (Fig. 2). From January onwards, dumps were more important than any other habitat type (Fig. 2). Furthermore, ricefields were unique in that gulls often remained there for more than one day before moving to a different site. This also varied seasonally, as 63% of the visits to ricefields that lasted for >24 h were in October–December.

3.2. Connectivity analysis

Based on centrality measures of "betweenness", ricefields (DR) were the most central node within the network, followed by three inland landfills in western (Rio Tinto, RTD), central (Montalbán, MoD) and eastern (Jaen, JD) Andalusia, and the Huelva coastal marshlands (HM) (Table 1). The two landfills (AGD and ARD) near the Doñana ricefields (DR) showed the highest number of direct flights in the connectivity network (Fig. 3; Table S1). Other examples of particularly strong connections between rubbish dumps and wetlands include the Antequera dump (AnD) with Fuente de Piedra (FPL) lake in Málaga, and Linares

Table 1
Details of the 37 LBBG sites selected for Andalusia, listing the habitat type, identity code (ID), location, surface area (km^2), relative time spent (%) in the site during the whole winter, mean January counts (when available, data for 2010–2017), and Betweenness Centrality (BC) values (number of shortest paths between other nodes that pass through a particular node). The top five values for each of area, relative time spent, mean counts and BC are highlighted in bold.

	Habitat type	ID	Location	Area (km^2)	% time spent	Mean counts	BC
1	Reservoir	GiR	Giribaile	37.01	**10.2**	972	158
2	Reservoir	NR	Guadalén	21.62	2.26	117	0
3	Reservoir	FR	Fernandina	22.72	0.33	1284	24
4	Reservoir	BR	Breña	34.60	1.64	**5286**	110
5	Reservoir	HR	Guadalhorce	39.65	0.31	656	0
6	Reservoir	LR	Limonero	2.69	0.11	–	0
7	Reservoir	AR	Andévalo	59.71	0.93	–	88
8	Reservoir	GrR	Grande	1.39	0.02	–	5
9	Reservoir	PR	Piedras	12.93	0.04	79	138
10	Reservoir	GeR	El Gergal	8.02	0.39	–	0
11	Reservoir	CBR	Corumbel Bajo	5.16	0.14	–	0
12	Lagoon	FPL	Fuente de Piedra	18.66	**12.08**	**18,690**	125
13	Lagoon	LEL	Lantejuela East	10.01	1.06	4172	4
14	Lagoon	LWL	Lantejuela West	3.64	1.36	1222	0
15	Port	MP	Malaga	3.51	0.74	–	69
16	Port	AP	Almeria	3.73	2.31	–	0
17	Ricefield	DR	Doñana	**493.28**	**43.00**	**10,800**	**454**
18	Coastal marsh	CGM	Cabo de Gata	9.44	0.13	302	4
19	Coastal marsh	PEM	Punta Entina Sabinar	34.12	0.06	1011	0
20	Coastal marsh	HM	Huelva	**177.46**	4.80	**5187**	**194**
21	Coastal marsh	CM	Bahia de Cadiz	**181.86**	0.01	**5882**	31
22	Coastal marsh	ICM	Isla Cristina	**62.36**	0.08	3366	3
23	Coastal marsh	RM	El Rompido	47.44	0.09	2082	111
24	Coastal marsh	BM	Barbate	25.30	0.02	346	0
25	Fish pond	VLP	Veta la Palma	**104.49**	0.34	284	0
26	Dump	RTD	Rio Tinto	1.15	1.85	–	**282**
27	Dump	AGD	Alcalá de Guadaira	2.69	**5.26**	–	99
28	Dump	ARD	Alcalá del Río	1.47	1.01	–	52
29	Dump	LD	Linares	1.31	**5.61**	–	0
30	Dump	JD	Jaen	1.32	0.08	–	**188**
31	Dump	BD	Breña	1.69	0.23	3536	68
32	Dump	MarD	Marchena	1.22	0.43	–	2
33	Dump	MoD	Montalban	1.26	1.22	3450	**267**
34	Dump	AnD	Antequera	1.46	0.71	–	34
35	Dump	AlD	Almería	0.94	0.34	–	4
36	Dump	MalD	Malaga	2.65	0.34	–	43
37	Dump	TD	Tharsis	1.08	0.44	–	33
Total				**1,439**	**100%**	**68,724**	

dump (LD) with Giribalde reservoir (GiD) in Jaén (Fig. 3, Table S1). With respect to connectivity between habitats, rubbish dumps are the habitats that hold the highest number of direct connections (90% of all direct flights) with wetlands (including reservoirs, ricefields, lagoons and marshlands), whereas only 7% of direct connections were between wetland habitats (Fig. 4, Table S2). In comparison, only 0.01% of direct connections were between exclusively terrestrial habitats (i.e. between dumps).

The number of connections between nodes declined significantly with the distance between them ($R^2 = 0.635$, $t = -2.346$, $p = 0.020$), and increased with the number of tagged gulls connecting those nodes ($t = 12.314$, $p < 0.0001$). Long-distance connectivity between sites was rare, as only 2% (115 of 5676) of the direct flights between nodes were beyond 60 km (Fig. S1). For example, there was just one direct flight between ricefields (DR) and Fuente de Piedra (FPL), the two sites where most gulls were counted.

Ten independent functional units (modules) were derived from the random walks algorithm, showing high rates of connectivity between

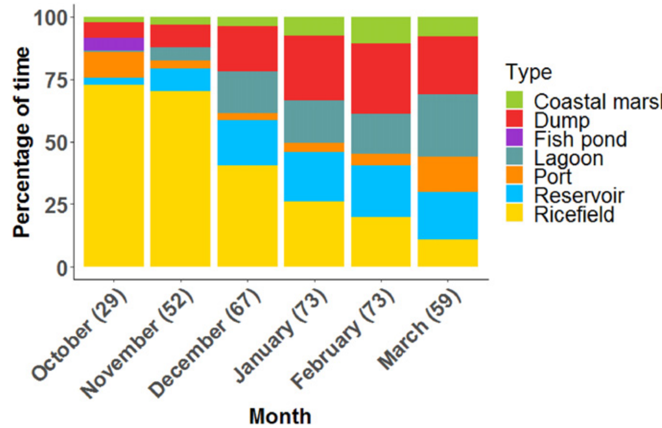

Fig. 2. Percentage of time spent by tagged gulls in different habitat types for different wintering months. The number of tagged bird-years is indicated in brackets (for 2010–2017).

the nodes within each unit, but low exchange between units (Fig. 3). Apart from unit 4 – which contained two coastal marsh sites – all other units contained at least one dump for foraging, and one natural or artificial wetland for roosting (Fig. 3). Functional units 3, 5, 6 and 7 in the central provinces of Seville, Malaga and Cordova were the most important for maintaining the connectivity from West to East within the study area (Fig. 3).

There were important temporal changes in the levels of connectivity within and between functional units during the course of the winter (Fig. 5). The number of flights was concentrated between December and February, peaking in January, and concentrated mostly within the functional units 3, 9 and 7, which were centred on ricefields, Fuente de Piedra and Jaen respectively. There was a steep decline in March, when the number of flights dropped within every functional unit as gulls began leaving their wintering quarters (Fig. 5).

4. Discussion

Waterbirds can act as biological connectors between habitat patches, providing functional connectivity between terrestrial and aquatic habitats. We showed that LBBG is highly mobile and uses diverse habitats while wintering in southern Spain, thereby functionally connecting coastal, terrestrial and aquatic habitats. Our study is unique in identifying the connectivity network of a species over such a broad scale (87,268 km^2). Functional connectivity for this species may be particularly high because it is, like most gull species, a generalist and opportunist that often travels long distances daily (Martín-Vélez et al., 2019; Thaxter et al., 2015). This functional connectivity can have major implications for the transport of nutrients and contaminants between sites, and for the dispersal of native and alien species able to survive gut passage, including pathogens (Lovas-Kiss et al., 2018, Martín-Vélez et al., 2019, Martín-Vélez et al., unpublished data).

4.1. Importance of the Doñana ricefields

The use (in terms of time spent) of different habitats by LBBG varied during the winter season. Ricefields were the most used habitat during the first months of the winter (October–December), but their use gradually decreased after November, while the time spent in other habitats such as rubbish dumps, reservoirs, lagoons and coastal marshes increased. This was expected given the seasonal changes previously observed in LBBG censuses in ricefields (Rendón et al., 2008). Because harvesting and tilling occur in the first half of the winter, gulls can then exploit food sources such as the alien red swamp crayfish and spilled rice grains (Lovas-Kiss et al., 2018; Toral et al., 2011).

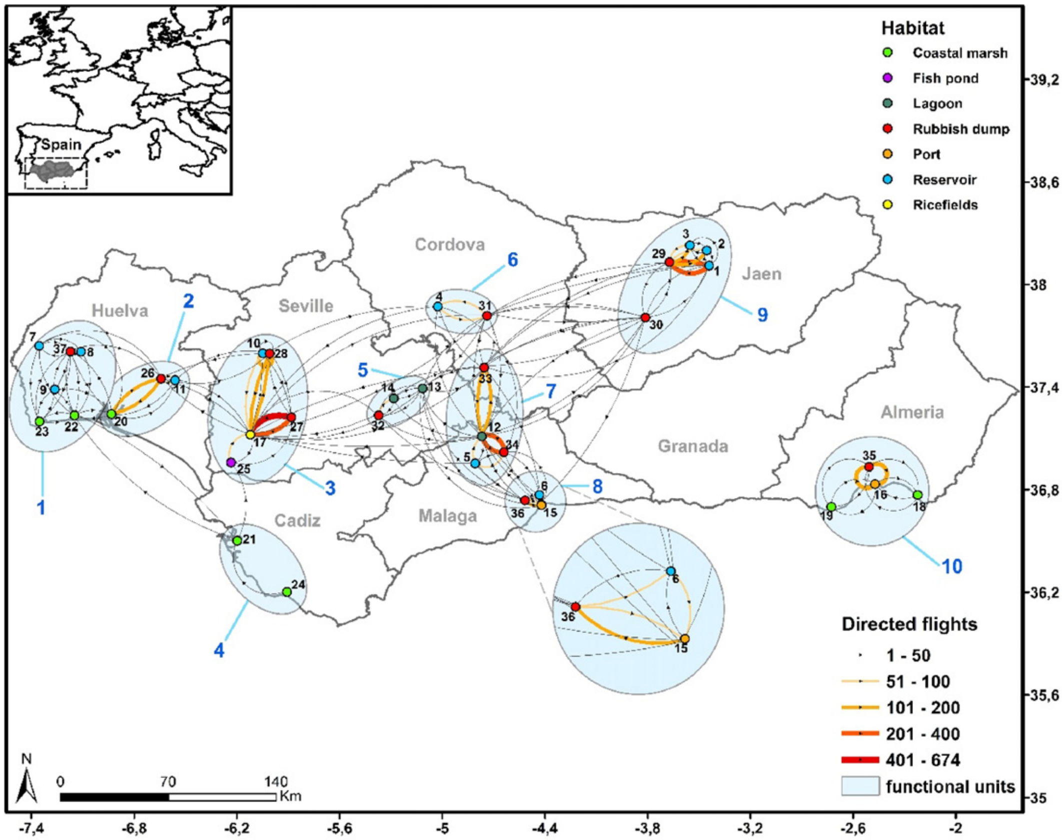

Fig. 3. Total connectivity by direct flights between sites (nodes coloured according to habitat type) within Andalusia from 2010 to 2017. Line width and colour of the arrows reflects the strength of the links in terms of number of direct flights (see Table S1 for full details). Light blue ellipses represent ten functional units (numbered in blue) within the connectivity network obtained from *infomap* clustering.

The Doñana ricefields is the largest of our study polygons, and can provide both roosting and foraging habitats at the same time, e.g. feeding in a paddy that is being harvested whilst roosting elsewhere on a dyke or in a different paddy that has already been harvested (Guzmán et al., 1999; Toral et al., 2012). The high availability and predictability of resources during the rice harvest provides food for large numbers of gulls, but also allows them to be relatively stationary in the same general environment (Masero et al., 2011). Thus, only 15% of the visits to the ricefields by gulls lasted >24 h, but these represented 69% of the total time spent in the ricefields. Nevertheless, some of these long visits were also made during the second half of the winter. This indicates that some gulls were still feeding there after harvest was completed, perhaps on waste grain or invertebrates available in the fields that remained flooded.

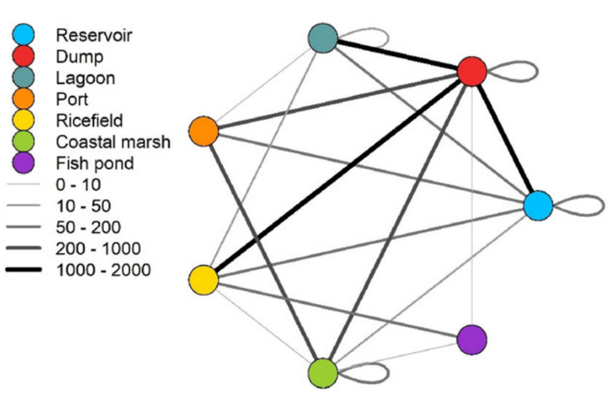

Fig. 4. Overall connectivity between different habitat types in Andalusia. Thickness and colour intensity of the line reflect the number of direct flights between all polygons of a given habitat type. See Table S2 for precise numbers of direct flights.

In contrast to the decrease in time spent within ricefield habitat as the winter advances, the importance of gulls for functional connectivity between ricefields and other habitats increased in the transition to late winter. Connections between and within functional units varied seasonally, with a peak between December and February, when the role of gulls as biovectors may be especially important. The gulls then start moving between different habitats, likely due to decreasing food availability in the ricefields (Toral and Figuerola, 2010; Toral et al., 2011), but may continue to use ricefields as a roosting site with daily visits to new foraging areas (Fujioka et al., 2010). These movements may also promote the spread of alien plant or animal species, which are particularly abundant in ricefields and whose propagules are dispersed by gulls at this time of year (Green, 2016; Lovas-Kiss et al., 2018). Ricefields also contain many weeds, which often have herbicide-resistant genotypes, and gulls leaving ricefields are likely to disperse them to other suitable habitats (Farmer et al., 2017; Lovas-kiss et al., 2018).

4.2. The key role of rubbish dumps in the connectivity network

If our only source of information about LBBG in Andalusia was the wintering waterbird census data from the wetland sites that are counted, we would have expected a high proportion of direct flights between those sites where most birds were counted (e.g. between the Doñana ricefields and Fuente de Piedra lake). However, our movement network shows that this is not the case. The 12 rubbish dumps were identified as key sites in the network, although ten of them are not included in the waterbird census. Overall, 90% of direct flights between nodes were made to or from a dump, providing a direct connection between a terrestrial and aquatic habitat. Dumps provide easy and

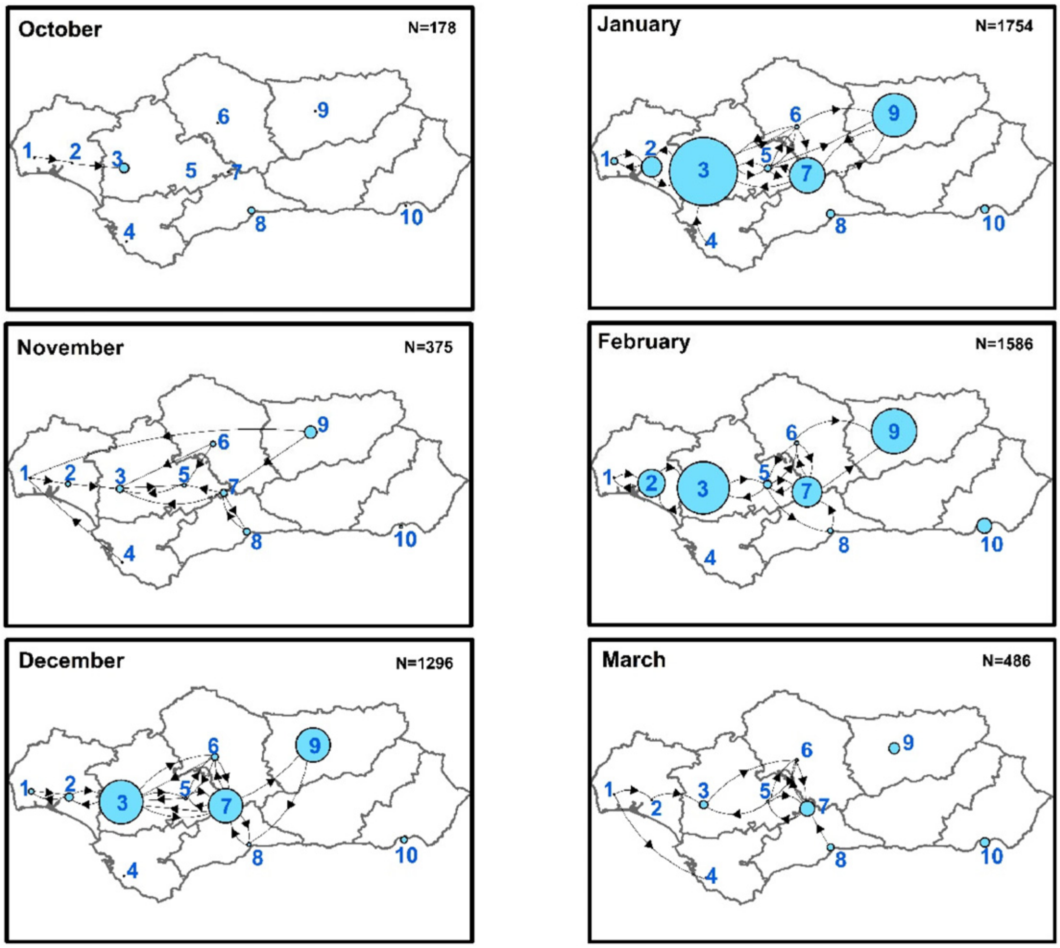

Fig. 5. Temporal change of connectivity between the ten functional units during winter months in Andalusia (data from 2010 to 2017). Size of the circles reflects the relative number of directed flights performed within a given functional unit, whereas arrows reflect direct connections between functional units. N in the top right hand corner refers to the total number of direct flights that month. See Fig. 3 for detailed information about functional units.

accessible resources without the need to expend much energy for searching (Duhem et al., 2005; Plaza and Lambertucci, 2017). For example, the rubbish dumps of Alcalá del Río (ARD) and Alcala de Guadaira (AGD) in the area surrounding the ricefields showed high connectivity with the ricefields themselves. Each functional unit contained complementary habitats, usually involving a major roosting site (reservoirs, lakes and other wetlands) and one or several foraging sites (ricefields, rubbish dumps or ports). Therefore, patterns of connections between rubbish dumps as foraging sites and wetlands as roosting sites are found along the connectivity network in most functional units (Fig. 3), and similar results were reported by GPS tracking of yellow-legged gulls *Larus michaellis* at a local scale within our unit 2 (Navarro et al., 2016). Although previous studies have shown the importance of the movement of marine nutrients onto land by birds (González-Bergonzoni et al., 2017; Irick et al., 2015; Sánchez-Piñero and Polis, 2000), our directed network shows that LBBG can transfer matter in the opposite direction: from inland rubbish dumps where they forage to coastal habitats where they roost, e.g. in functional units 2, 8 and 10 (Fig. 3).

Movement of gulls transporting nutrients into lakes and reservoirs from rubbish dumps occurs across North America, and causes important eutrophication effects (Winton and River, 2017). Such guanotrophication is also a major process in Andalusia, and nutrient inputs by LBBG have been quantified for Fuente de Piedra (Martín-Vélez et al., 2019). This current study shows the importance of many dumps in the same region, and how they are interconnected. Similarly, gulls using rubbish dumps can play an important role in biovector pathways of conventional and emerging contaminants (e.g. plastics, Persistent Organic Pollutants[POPs]) and heavy metals into natural ecosystems and into the human food chain (Desjardins et al., 2019; Kapelewska et al., 2019; Michielsen et al., 2018). LBBG wintering in Andalusia are known to carry a range of bacteria with Antimicrobial Resistance (AMR) genes (D. Jarma et al. unpublished data). As rubbish dumps are one of the most important sources for AMR (Arnold et al., 2016; Ramey et al., 2018), the direct movements of gulls between rubbish dumps and reservoirs, ricefields and ports may be of concern. This study provides a valuable step towards identifying specific pathways for AMR transmission by birds in Andalusia (see Arnold et al., 2016 for general AMR pathways).

4.3. Dispersal of plants and other organisms

Functional connectivity by LBBGs is mainly limited to within 60 km because only a small proportion of direct flights within Andalusia are longer. Nodes were aggregated in the functional units by proximity, which suggests connectivity was limited by distance, and connectivity between functional units was relatively low. Nevertheless, LBBG in Andalusia disperse many plants and invertebrates by endozoochory that would otherwise only be able to disperse over much shorter distances (Lovas-Kiss et al., 2018). The connectivity network indicates that gulls make excellent vectors for stepping stone dispersal around Andalusia, in which novel organisms with a broad niche can be spread gradually around Andalusia by LBBG vectors. We also found that 7% of direct flights occur between different wetlands such as the ricefields, reservoirs, natural lakes and coastal marshes, and these connections may facilitate the dispersal of aquatic plants and invertebrates between localities, including alien bryozoans, snails and other invertebrates shown to survive gut passage by gulls (Lovas-Kiss et al., 2018, Martín-Vélez et al. unpublished data).

4.4. Implications for management

This study demonstrates how connectivity among wetland habitats can be indirectly stimulated by connections between aquatic and terrestrial habitats: because gulls are using rubbish dumps they are indirectly also increasing connectivity among inland wetlands. Our study further strengthens the notion that the growth in numbers of LBBGs on inland wetlands is the result of the expansion of rubbish dumps in Southern Spain, as previously reported for the UK (Harris, 1970). Long-term census data at Fuente de Piedra lake showed that LBBG have only become numerous in the past 30 years since landfills appeared (Martín-Vélez et al., 2019). The expansion of ricefields in recent decades is also likely to have directly contributed to the increase of the wintering gull population, but our study shows that this is also partly because ricefields are a preferred roost site for gulls feeding at dumps.

This study provides a major insight into the likely pathways of biovectoring from rubbish dumps. By identifying connections with key landfills, it can help to plan future studies of contaminant transport and develop management measures to reduce guanotrophication and contamination issues, helping to protect biodiversity and water quality at key natural wetlands and reservoirs. A new National Framework Waste Management Plan (Plan Estatal Marco de Gestión de Residuos, 2015), based on the Landfill Management Directive, was approved in Spain in 2015 for the period 2016–2022. This directive requires the gradual reduction of biodegradable waste to 35% in 2016, with a further reduction of an additional 35% in 2020, as well as measures to improve waste separation and recycling. Such measures could potentially reduce the number of gulls at landfills and control the main pathways of terrestrial-aquatic connectivity and hence potential contamination.

This study demonstrates how gull movements provide important aquatic-terrestrial linkages. These are of great importance (Soininen et al., 2015), yet largely overlooked by the international community responsible for wintering waterbird censuses. There is great value in integrating studies of movement ecology with conventional waterbird surveys, because only the combination can provide a clear understanding of the connectivity between sites used by waterbirds. Based on movement data, key sites that lack survey data can be identified. Gull movement data suggests that counts at wetlands can be severely underestimated by missing birds that have flown to landfills (Martín-Vélez et al., 2019). This study identified many important sites that are not covered by waterbird counts, which can help to improve future censuses. Our results suggest that the total number of LBBGs in Andalusia is likely to be much higher than that estimated from January counts (see Table 1).

4.5. Further work

Analyses like ours allow the scaling down of complex movements to a reduced set of nodes. Using a multi-state model framework, more specific covariates (e.g. age, sex or natal origin of gulls) could be incorporated in the future to identify key drivers of movement between nodes (e.g. Fremgen et al., 2017), and potentially also drivers of survival rates. Further studies should also address connectivity at different scales. Here we focused on connectivity at a regional scale, but focusing at more local scales may uncover new nodes and connections, and identify movements between other terrestrial and aquatic habitats of importance for biovectoring (e.g. the transport of weeds in agricultural land, or the transport of AMR into urban areas with risks for human health). On the other hand, network and connectivity analyses should also be applied to LBBGs in their breeding range. By assessing how stable such networks are through time, such analyses may help to identify critical breeding areas and enhance their conservation. Furthermore, the contribution of different LBBG individuals in connectivity networks should be investigated, as their roles may differ greatly. Specialist individuals may remain within a single functional unit throughout the winter, whereas more versatile, generalist individuals may have a more important role in both inter-habitat and long distance connectivity (between functional units).

5. Conclusions

LBBG provide important connections between terrestrial and aquatic habitats due to their high mobility and generalist behaviour. Doñana ricefields and various rubbish dumps performed as central nodes to maintain connectivity in the whole Andalusian region, although such connections changed seasonally together with changes in habitat use. High connectivity implies transport of organisms, nutrients, resistance genes and contaminants between different habitats by LBBG biovectors. Most transport occurs within 60 km distance and within ten functional units. This study has identified a unique multi-scale connectivity network between terrestrial and aquatic habitats, with important management implications.

Author contributions

V. Martín-Vélez: Formal analysis, Visualization, Roles/Writing - original draft, Conceptualization, Methodology; B. Mohring: Methodology, Software, Data curation; C.H.A. van Leeuwen: Writing – Review & Editing; J. Shamoun-Baranes: Resources, Investigation, Writing – Review & Editing; C. Thaxter: Resources, Investigation, Writing – Review & Editing; J.M. Baert: Resources, Investigation, Writing – Review & Editing; K. Camphuysen: Resources, Investigation, Writing – Review & Editing; A.J. Green: Conceptualization; Funding acquisition; Methodology; Supervision; Writing, Review & Editing.

Declaration of competing interest

Authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2019.135886.

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