



Gulls living in cities as overlooked seed dispersers within and outside urban environments

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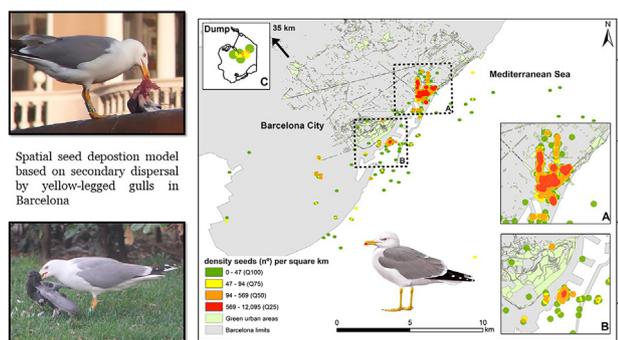
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HIGHLIGHTS

- Urban gulls transport seeds within cities by primary and secondary dispersal.
- Seed dispersal through pellet deposition was spatially modelled for the first time.
- Seven alien plant species were reported for seed dispersal within Barcelona.
- Around 30% of the seeds dispersed were deposited at suitable green urban areas.

GRAPHICAL ABSTRACT



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ABSTRACT

The yellow-legged gull is an opportunistic and generalist bird that has colonised urban areas, where it has found very favourable trophic resources but also causes disturbance to humans and damage to infrastructure. Here, we investigated the potential role that gulls play in the dispersal of plants in Barcelona, a highly populated city of north-eastern Spain. We analysed the stomach contents of 145 chicks collected in urban nests and reported the presence of seeds of 27 plant taxa. We then developed a plant dispersal model based on the movements of 20 GPS-tracked yellow-legged gulls breeding in the city of Barcelona. We estimated seed dispersal distances, seed shadows and percentage of seeds reaching habitats suitable for seeds regurgitated in pellets and those excreted in faeces. Seven of the 27 plant taxa found in the stomachs were alien taxa to Spain. Average dispersal distances of plant seeds by gulls were around 700 m, but maximum dispersal distances reached up to 35 km. Dispersal distances and seed spatial patterns did not differ between faeces and pellet models, as most strongly depended on gull movements. About 95% of the seeds were dispersed within urban environments and between 20 and 30% reached suitable habitats for seed deposition (urban woodlands, green urban parks and urban grasslands). Urban gulls frequently dispersed seeds (including alien species) within urban habitats, both via direct consumption or via secondary dispersal after consuming granivorous birds that had ingested the seeds, such as pigeons or parakeets. Urban planning for Barcelona is based on native plant species, and thus, special attention should be paid to alien plants dispersed by birds, which could pose a risk to native biodiversity in urban ecosystems.

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1. Introduction

The effects of urbanisation on different bird species are variable (Sol et al., 2013; Méndez et al., 2020). While many species are unable to adapt to the human impacts associated with cities, others have found a window of opportunity in city life (McKinney and Lockwood, 1999). Urban ecosystems provide stable, accessible food resources and less predation pressure than natural environments for those species able to adapt to cities (Lim and Sodhi, 2004; Palomino and Carrascal, 2007; Méndez et al., 2020; Leveau, 2018). Some urban bird species (e.g. house sparrow *Passer domesticus*) are completely adapted to urban environments without being a nuisance to city managers (Thearle, 2013). However, conflicts with humans are associated with other birds adapted to urban environments, resulting from noise pollution, damage to infrastructure and transmission of pathogens (Navarro et al., 2019; Vergara et al., 2017; Senar et al., 2016; Belant, 1997).

Gulls are a clear example of opportunistic birds adapted to urban environments both for breeding and foraging (Spelt et al., 2019; Rock et al., 2016; Méndez et al., 2020). The presence of a wide variety of trophic resources, including human-related ones, within cities lead to the establishment and growth of urban gull populations worldwide (Washburn et al., 2013; Spelt et al., 2019). The number of gulls nesting on roofs is increasing, creating problems for residents, including defecation, obstruction of drain systems, structural building damage, harassment, airplane collisions and disease transmission (Belant, 1997; Vidal et al., 1998). Methods for controlling urban gull populations include disturbance to birds, management of nesting areas or food sources (from landfills or ports), or direct removal of adult birds (Belant, 1997).

Urbanisation is a major factor promoting biological invasions worldwide, because highly disturbed habitats provide ecological niches for alien species. Moreover, cities often act as gateways to alien invasions through airports, harbours, highways, and train stations, whereas gardens and urban parks can become sources of propagules for spreading to natural areas (Farelo et al., 2017). A main feature of the urban flora is the high proportion of non-native species (van Heezik et al., 2012). Many alien plant species were introduced intentionally within the cities for economic and ornamental purposes (Czarnecka et al., 2013), and invasive species colonising natural habitats can negatively affect green urban planning efforts (Štajerová et al., 2017; Gaertner et al., 2016).

Zochoorous seed dispersal is another way that non-native species can spread. A little-studied impact of gull species in cities is their potential to redistribute plant species both within urban patches and beyond urban environments (Calviño-Cancela, 2011). The provisioning of anthropogenic food resources available in cities such as agricultural crops, orchards, gardens or plantations provide exploitable resources to bird species (Sengupta et al., 2021), with the potential for primary seed dispersal by direct consumption of seeds or secondary seed dispersal through the consumption of other granivorous bird species. Seed dispersal within cities may be especially relevant when the plants dispersed by birds are invasive or alien, as previously stated (Corlett, 2005; Li et al., 2017).

The yellow-legged gull *Larus michahellis* is known to disperse a wide variety of plants through primary endozoochory (Nogales et al., 2001; Calviño-Cancela, 2002). Secondary seed dispersal by the black-backed gull *Larus fuscus* feeding on the American red crayfish *Procambarus clarkii* (Lovas-Kiss et al., 2018a; Martín-Vélez et al., 2021a) may result in dispersal distances beyond 150 km for alien and weed plant species (Martín-Vélez et al., 2021b). The proliferation of urban populations of yellow-legged gulls inhabiting the city of Barcelona can have important implications for seed dispersal, both through direct plant consumption or through secondary seed dispersal (Calviño-Cancela, 2011). In addition to the consumption of marine resources, urban bird species such as rock pigeon *Columba livia* and monk parakeet *Myiopsitta monachus* have been described as important prey for this opportunistic gull (Méndez et al., 2020). Rock pigeon and monk parakeet are known to forage on a wide range of urban plant species (e.g. alien and ornamental species) within cities (Spennemann and Watson, 2017; Borray-Escalante et al., 2020).

Seed dispersal within urban landscapes by gulls has never been studied. Barcelona is a good system to study the potential for seed dispersal and the spatial patterns of seed dispersal deposition within the city. Furthermore, new technology using GPS tracking devices with yellow-legged gulls in Barcelona can provide reliable bird movements information (Méndez et al., 2020) to generate spatial models of seed dispersal (e.g. Bartel et al., 2018). In the present study, we aimed to (1) characterise the plant taxa that can be dispersed by yellow-legged gulls breeding and foraging in an urban environment, including whether they were alien species and (2) determine the dispersal distances and spatial seed shadows generated by yellow-legged gulls in Barcelona.

2. Materials and methods

2.1. Fieldwork procedures

The study was developed during the breeding season (May to June) from 2018 to 2021 in the city of Barcelona (north-east Spain, Fig. 1A), a coastal urban area considered the eighth and second largest city of Europe and Spain, respectively (1,600,000 inhabitants). The yellow-legged gull urban population of Barcelona has estimated as around 300 breeding pairs (Antón et al. 2017). The climate of Barcelona is dry and warm in summer and mild and wet during winter with long periods of sunlight throughout the year. The warmest months- are July and August (22–28 °C), while January and February (8–11 °C) are the coldest months (Algeciras and Matzarakis, 2016).

To determine the presence of seeds, we analysed the stomach contents of 145 chicks of yellow-legged gulls collected in 145 different nests throughout the urban area of Barcelona (Fig. 1B and C). Stomachs were frozen at –20 °C until processing in the laboratory. No chicks were specifically killed for this study because all individuals were provided by the Public Health Agency of Barcelona after they were euthanized (Pest Management Plan of Barcelona; Legislative Decree 2/2008 of April 15th, DOGC).

To examine the movements of the yellow-legged gulls, during the breeding seasons of 2018 and 2019, 20 breeding adults (that presented incubation patch indicating that were actively breeding) were captured in a baited trap installed in Barcelona and were tagged with 2 different GPS units (12 individuals tagged with GPS-WIMBISF-25 manufactured by Wimbitek SL and 8 individuals tagged with GPS-CatLog manufactured by Perthold Engineering LLC; Table 1). Each GPS units had different frequency of GPS data recording (every GPS-WIMBISF-25 30 min for GPS-WIMBISF-25 and 10 or 5 min for GPS-CatLog during 2018 or 2019, respectively). Moreover, the methodology of obtaining the GPS data differed between GPS-WIMBISF-25 units (the data was retrieved remotely by using SigFox network) and GPS-CatLog units (the data was downloaded directly from the logger). All GPS units were deployed using a wing harness (Thaxter et al., 2014). The GPS unit and harness weighed less than 2% of the body mass of the tracked gulls (GPS-WIMBISF-25 = 21 g, GPS-CatLog = 16 g; mean \pm SD of instrumented yellow-legged gulls = 1011.23 \pm 125.45 g), below the 3% body mass threshold suggested for gulls (Phillips et al., 2003; Passos et al., 2010).

2.2. Stomach content analysis

Stomachs were unfrozen and processed under laboratory conditions during March and December 2021. The stomach contents were inspected in Petri dishes and all intact seeds were retrieved, counted, photographed and measured with ImageJ software (Schneider et al., 2012). We identified them to the lowest taxonomic level by comparing the shape, size and seed coat pattern to information in the available literature (Bojnanský and Fargašová, 2007; Cappers et al., 2012). When it was not possible to assign an item to a species with certainty, genus or family level was reported. We also classified the identified seeds as native or alien, based on Aymerich and Sáez (2019). In addition to the seeds, the major prey groups

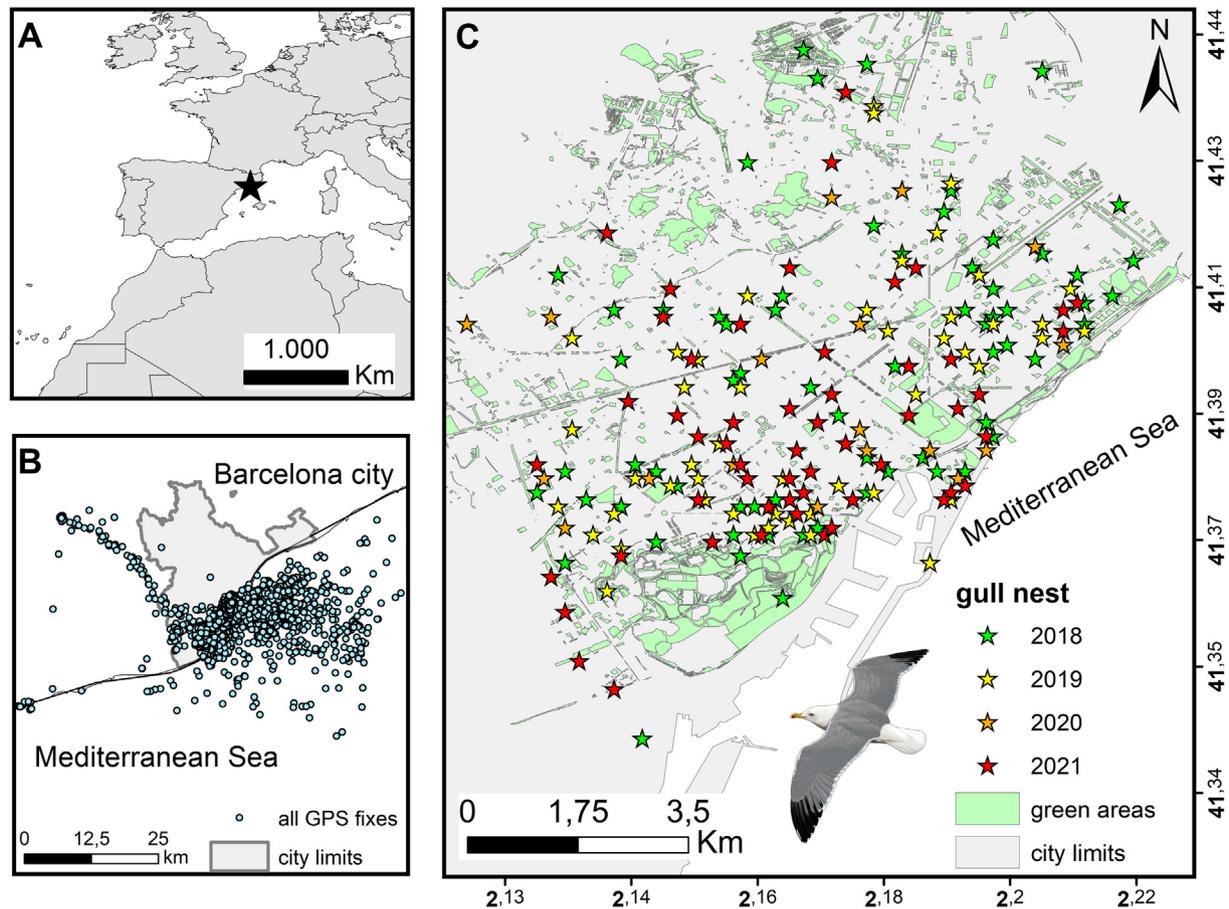


Fig. 1. A) Location of Barcelona city within Europe. B) GPS positions (blue circles) of 20 GPS-tracked yellow-legged gulls during the 2018–2019 breeding season in Barcelona. C) Distribution of the 145 nests sampled in Barcelona during the 2019 breeding season to examine the stomach contents of the yellow-legged gull chicks. The draw of yellow-legged gull was made by Martí Franch.

(e.g. rock pigeon, monk parakeet or fish; Méndez et al., 2020) were identified when possible, photographed and counted (at the smallest number possible).

Table 1

Summary of the data included in the analyses from 20 tagged gull-year individuals breeding in the city of Barcelona during the breeding seasons of 2018 and 2019. Individual gull identification (ID), GPS model, date of the first and last GPS location, total duration of the track and total number of locations are shown.

ID	GPS model	Date of first GPS location	Date of last GPS location	Total duration (days)	Total locations
PBMM	CatTrack	11/05/2018	13/06/2018	33	3126
PBTP	Wimbitek	17/05/2018	30/06/2018	44	1786
PBWB	Wimbitek	17/05/2018	30/06/2018	44	1174
PXTZ	Wimbitek	17/05/2018	25/06/2018	39	1405
PXZS	CatTrack	09/05/2018	25/06/2018	47	1515
PYAB	CatTrack	26/04/2018	09/05/2018	13	1219
PYFL	CatTrack	11/06/2018	30/06/2018	19	1885
PYHS	CatTrack	26/04/2018	30/04/2018	4	402
PZYL	CatTrack	04/06/2018	30/06/2018	26	2533
PBLZ	Wimbitek	08/05/2019	30/05/2019	22	842
PBMM	Wimbitek	01/04/2019	30/06/2019	90	1540
PBSF	CatTrack	10/04/2019	15/05/2019	35	4337
PBWB	Wimbitek	08/04/2019	30/06/2019	83	1886
PXJS	Wimbitek	07/05/2019	30/06/2019	54	2035
PXMC	Wimbitek	26/04/2019	30/06/2019	65	2849
PXXT	Wimbitek	05/04/2019	23/06/2019	79	2494
PXZY	Wimbitek	26/04/2019	30/04/2019	4	207
PZZC	CatTrack	30/04/2019	18/05/2019	18	5073
PXXT	Wimbitek	09/04/2019	15/05/2019	36	620

2.3. GPS data analysis

For the spatial movement analysis, we used the following parameters recorded by the GPS loggers: date, time of day (UTC), latitude, longitude and instantaneous speed, and the body mass of each GPS-tracked gull. We calculated additional variables from the raw parameters: haversine distance between fixes, time difference between GPS points (calculated from forward intervals between consecutive GPS points set up between 15 and 30 min) and trajectory speed ($\text{km}\cdot\text{h}^{-1}$). To simulate the start of a gull trajectory, we selected all GPS fixes within the limits of Barcelona city (Fig. 1). Additionally, we selected only GPS fixes that also overlapped with the distribution of their main urban prey (rock pigeons and monk parakeets; Anton et al., 2017) known to be consumed extensively by yellow-legged gulls breeding in Barcelona (Méndez et al., 2020) during the day (from 07:00 to 19:00 h UTC). This time range excluded the main roosting periods and feeding at sea during night when seed ingestion was less probable. The GPS fixes within Barcelona under those requirements correspond to a total of 706 gull-day trajectories from a combination of the 20 tracked gulls (Table 1).

2.4. Seed deposition modelling

Faeces deposition was simulated based on a seed retention curve derived from an allometric equation (Eq. (1)) which relates mean retention time to body mass across bird species (Yoshikawa et al., 2019):

$$\begin{aligned} \text{Log}_{10} \text{ mean seed retention time (min)} \\ = 0.631 + 0.561 * \text{log}_{10} \text{ body mass (g)}. \end{aligned} \quad (1)$$

We used a mean and standard deviation body mass of 1006 ± 136 g (based on the body mass of the 20 GPS-tracked yellow-legged gulls), and extracted a mean retention time of 3.44 h (Eq. (1)). We then generated a lognormal retention time distribution from a shape (sdlog) and a scaling (meanlog) parameter (Viana et al., 2016). The scaling parameter was calculated from the mean retention time derived from Eq. (1), and the shape parameter is fixed at 0.7 (using the *rlnorm* function in R by random generation), as proposed by Viana et al. (2016) for endozoochory relationships (Fig. 2).

One of the 706 gull-days was randomly selected and assumed that the seed ingested at time $t0$ was randomly assigned to an hour between 07:00 and 19:00 h. Based on the retention time curve, we randomly selected a retention time $t1$ when the seed would be excreted, based on the density probability curve through the *sample* function in R (v3.6.3 R Core Team, 2020). The location of seed egestion was calculated based on the GPS coordinates at $t1$, and the Haversine distance between GPS points at $t0$ and $t1$ where the seed was dispersed was calculated through *deg.dist* function in *fossil* R package. We performed the modelling to simulate pellet deposition from $t0$ until $t1$, with pellet deposition $t1$ being the first GPS point from the random trajectory when the gull was resting and not flying and beyond 9.5 h, the time that yellow-legged gulls take to produce animal pellets in captivity (Nogales et al., 2001). We repeated these randomizations 1000 times for each excrement and pellet modelling and assumed each excreta contained 1 intact seed. Therefore, each model simulation represented the dispersal of 1000 seeds in the study area. Differences between dispersal distances in seed models were analysed through Wilcoxon U non-parametric test being $\alpha = 0.05$. Each faeces accounts only for 12.5% of total daily faecal output in gulls (Hahn et al., 2007), and the number of gulls in Barcelona is above 1000 (Anton et al., 2017). Therefore, faecal simulation represented only a fraction (roughly 25%) of the number of viable seed dispersal events by yellow-legged gulls in a day.

We generated a spatially explicit seed deposition map in the city. First, we generated a density map (in seeds km^{-2}) considering a 100 m neighbouring area of influence around each seed deposition point estimated from the

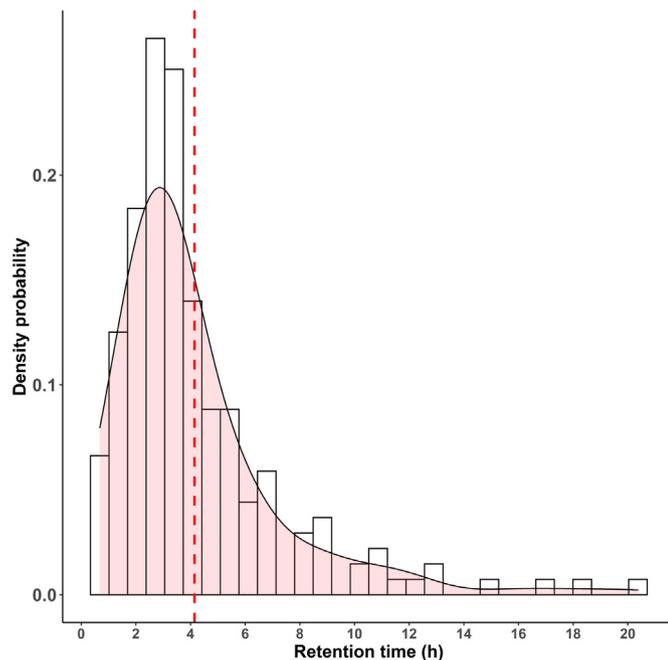


Fig. 2. Theoretical curve based on 3.44 h mean retention time (calculated from Eq. (1)) and a lognormal curve with $\text{sdlog} = 0.7$ corresponding to the shape of the curve derived from random sampling ($N = 100$) (after Viana et al., 2016). Red dashed lines indicate the mean retention time estimated from the random generation as 4.1 h (with shape 0.7).

model for a correct visualization. We used the Point Density tool from ArcMap 10.1 with a final spatial resolution of 10 m. We calculated seed density maps for each model separately (pellet and faeces) and then summed the two outputs to perform a final model based on pellets and excrement together. Areas with a high probability of seed deposition were selected by considering those areas enclosing the 25%, 50% and 75% quantile values from the final seed model. Furthermore, crossed this seed deposition map with the land use information (scale 1:2000, year 2020) from Catalonia (Ibáñez et al., 2002). This allowed us to determine the seven main habitat types into which seeds would be dispersed: (1) port, (2) waste dump, (3) beach and sea, (4) urban woodland, (5) green urban area, (6) other urban area and (7) grassland. From these, we only considered urban woodland, green urban area and grassland as potential areas suitable for successful seed establishment after dispersal. Finally, areas with higher probability of successful dispersal were delimited as those previous areas with a high probability of seed deposition that had habitats suitable for seed establishment. The software ArcMap 10.1 (ESRI, Redland, USA) and RStudio 4.0.3 (RStudio Team, 2020) were used to perform this spatial analysis.

3. Results

3.1. Stomach contents

Of the 145 stomachs analysed, 91 (63%) contained rock pigeon, 63 (43%) contained fish and 19 (13%) contained signs of small rodents. There were signs of garbage (mainly plastic) but no invertebrates. Forty-five out of the 145 stomachs analysed (31%) contained seeds, 30 of which (66.7%) also contained rock pigeons. An average of 0.85 seeds per stomach was found with a maximum of four different plant taxa found in two samples. A total of 27 different plant taxa and 124 seed items were found in the stomach samples, seven of them considered species alien to Spain (Table 2). Twenty-one of the ten taxa were associated with rock pigeon remains in the stomach samples (Table 2). Rarefaction analyses revealed a steep slope, suggesting that increasing sample size will increase the number of plant species present in the stomach content of yellow-legged gull chicks (Fig. S1).

3.2. Seed dispersal modelling

We did not find differences in the dispersal distances recorded between the 20 GPS-tracked yellow-legged gulls (Wilcox chi-squared = 511,272, $p = 0.32$). The mean dispersal distance of 1000 seeds from randomizations based on faecal retention times was 0.77 km with a maximum of 35.71 km (Table 3, Fig. 3). Mean dispersal distance for seeds egested via pellets was 0.86 km with a maximum of 35.68 km (Table 3, Fig. 3). Median distance was 0.07 km for faeces model and 0.07 km for pellets model (Table 3; Fig. 3).

Approximately 95% of the seeds deposited by both faeces and pellet models fell within Barcelona city boundaries. Areas with the highest densities of deposited seeds (up to $12,095$ seeds km^{-2}) were restricted to an urban park area within Barcelona city, where adults were captured (Fig. 4A) and the areas close to an urban hill and a fishing and industrial port area (Fig. 4B). Sixty percent of the highest density area (25% quantile corresponding to the red area in Fig. 4) was related to other urbanised habitats, whereas approximately 20 and 10% were related to woodland urban areas and green urban areas, respectively (Table 4). Fifty-two percent of the total modelled seeds dispersed by either pellets or faeces were deposited within the urban area of Barcelona not suitable for seed establishment. However, around 20% of the seed densities fell within a suitable green area within Barcelona, including urban woodland (9.8%), grasslands (3.37%) and green urban zone (7.01%) (Table 4). The remaining seeds were deposited within the Barcelona port at the beach or directly at sea (2.1% of the total seeds). Seeds that travelled the farthest (1.91% of them) were deposited in a dump, 35 km away from Barcelona city (Fig. 4C).

Table 2

Details of the taxa of plants with intact seeds found in the stomachs of the chicks of yellow-legged gulls sampled from 2018 to 2021 in the city of Barcelona. For each taxon, the association with a prey item (e.g. rock pigeon), the native status of the plant taxa to Spain according to Aymerich and Sáez (2019), the number of samples in which the taxon was recorded (NST), the combined number of seeds in those samples (N total seeds) and the maximum of seeds recorded per taxa is given.

Family	Species	Presence of bird as prey	Native species	NST	N of seeds	Max seed per sample
Actinidiaceae	<i>Actinidia deliciosa</i>	No	No	1	1	1
Arecaceae	<i>Washingtonia robussta</i>	Yes	No	2	10	9
Brassicaceae	<i>Coronopus squamatus</i>	Yes	Yes	1	14	14
Brassicaceae	–	Yes	–	1	1	1
Cannabaceae	<i>Celtis australis</i>	No	Yes	1	1	1
Convolvulaceae	<i>Cuscuta cf. campestris</i>	Yes	No	2	6	3
Cucurbitaceae	–	Yes	–	1	1	1
	<i>Tetragonolobus maritimus</i>	Yes	Yes	2	6	4
Fabaceae	<i>Trifolium repens</i>	Yes	Yes	1	1	1
Fabaceae	<i>Trifolium sp.</i>	Yes	–	1	2	2
Juncaceae	<i>Juncus sp.</i>	No	–	1	3	3
Lythraceae	<i>Lythrum cf. salicaria</i>	No	Yes	1	1	1
Moraceae	<i>Ficus carica</i>	Yes	No	1	1	1
Oleaceae	<i>Olea europaea</i>	Yes	Yes	3	3	1
Plantaginaceae	<i>Veronica sp.</i>	Yes	–	2	1	1
Poaceae	<i>Setaria viridis</i>	Yes	Yes	1	1	1
Poaceae	<i>Echinochloa crus-galli</i>	Yes	No	8	52	37
Poaceae	<i>Echinochloa sp.</i>	Yes	–	1	1	1
Poaceae	<i>Oryza sativa</i>	Yes	Yes	1	1	1
Polygonaceae	<i>Polygonum aviculare</i>	No	Yes	1	1	1
Ranunculaceae	<i>Ranunculus arvensis</i>	Yes	Yes	1	3	3
	<i>Ranunculus trichophyllus</i>	No	Yes	1	3	3
Ranunculaceae	<i>Ranunculus baudotii</i>	Yes	Yes	1	1	1
Rubiaceae	<i>Galium sp.</i>	Yes	–	2	3	2
	<i>Solanum chenopodioides</i>	Yes	No	1	1	1
Solanaceae	<i>Solanum eleagnifolium</i>	Yes	No	1	1	1
Urticaceae	<i>Urtica dioica</i>	Yes	Yes	1	4	4
	Total				124	

4. Discussion

In the present study, we present for the first time a spatial analysis of the seed shadows and dispersal services provided by an urban living population of yellow-legged gulls. While this dispersal service may have positive effects on the maintenance of connectivity and biodiversity, it also has potential negative effects because many of the dispersed plant species were alien, some with invasive potential presenting a possible risk for natural habitats.

4.1. Stomach contents and seed dispersal potential

The rock pigeon was the most frequently identified prey item followed by fish remains, as previously reported by Méndez et al. (2020) for the same area in previous years. The main novelty of our study is the detection of secondary dispersion of seeds by yellow-legged gulls. Moreover, 78% plant taxa reported in the study were found together with urban bird remains that served as prey for gulls. Most of the plant species reported do not have a fleshy fruit, supporting previous evidence that gulls are effective seed dispersers of non-fleshy fruited plants (Martín-Vélez et al., 2021a).

Table 3

Comparison between models builds from faeces and pellet retention time curves, presenting dispersal distances (in km, means, quantiles and maximum distances). Note 50% quantiles are the medians.

Model	Dispersal distance (km)				
	Mean	25%	50%	75%	Max
Faeces	0.77	0.02	0.07	0.39	35.71
Pellet	0.86	0.02	0.07	0.40	35.68

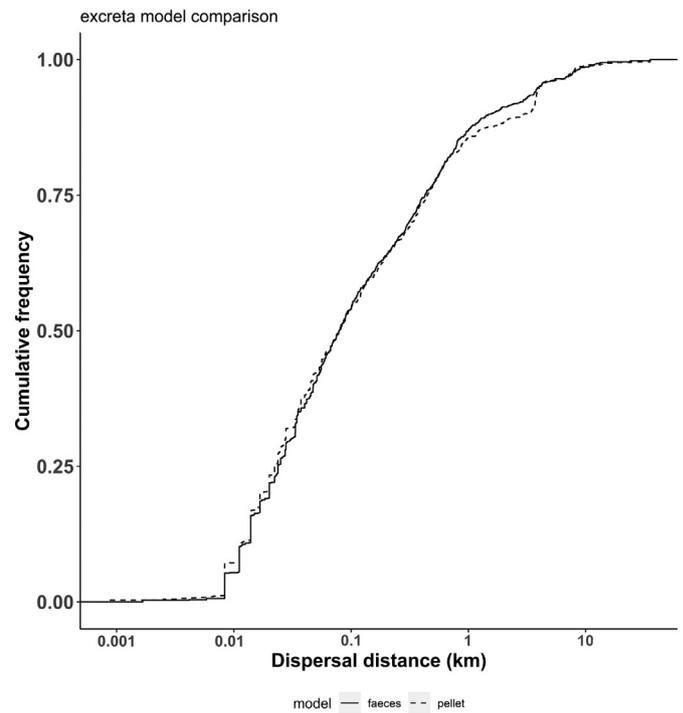


Fig. 3. Cumulative frequency distributions of dispersal distances (km) obtained from excreta models build using faeces (solid line) and pellet (dashed line) retention time curves, with a log scale on the X-axis based on 1000 random seeds modelled.

Given the small size of the seeds dispersed and the abundant prey item remains in the samples, a secondary seed dispersal mechanism is the most likely explanation, as has been reported previously for other gull species (e.g. *Larus fuscus*; Lovas-Kiss et al., 2018a). On the other hand, *Ficus carica*, *Actinidia deliciosa*, *Oliva europaea*, *Celtis australis*, *Washingtonia robussta* and *Solanum* spp. present fleshy fruits which may be ingested actively by yellow-legged gulls. Other studies have reported an active ingestion of other fleshy fruits by gulls (e.g. *Ruppia fruticosa*, *Corema album*; Nogales et al., 2001, Calviño-Cancela, 2002), olives (Calviño-Cancela, 2011), and they have been observed consuming fruits of *Washingtonia robusta* in Barcelona (Raül Aymí, personal observation, Fig. S2).

Unfortunately, we could not test the viability of these seeds in the current study because the gull stomachs were frozen for months before analysis. Previous studies have reported that many of the plant species reported in this study were previously dispersed by other birds. For example, *Ficus carica* was reported in faecal samples of mallards (*Anas platyrhynchos*) and ravens (*Corvus corax*) (Lovas-Kiss et al., 2018b; Nogales et al., 1999). *Echinochloa crus-galli* was reported germinate after being dispersed by mallards (Wongsriphuek et al., 2008). *Trifolium repens* was reported to be secondarily dispersed by white storks through pellets (Martín-Vélez et al., 2021a). Plant species from the genera *Solanum* spp. and *Ranunculus* spp. germinated after being secondarily dispersed by lesser black-backed gulls *Larus fuscus* in South Spain (Lovas-Kiss et al., 2018a; Martín-Vélez et al., 2021a). Therefore, the potential for those plant species to be successfully dispersed by yellow-legged gulls in Barcelona is very high.

4.2. Model comparison and dispersal distances

Models parametrised for faecal and pellet dispersal generated similar dispersal distances for yellow-legged gulls. To the best of our knowledge these are the first spatial dispersal seed shadows generated for pellets, as previous seed dispersal models based on GPS movements in waterbirds were focussed only on faeces deposition (Martín-Vélez et al., 2021b; Kleyheeg et al., 2017). Here, we show that pellet dispersal distances may be as far as faecal deposition distances, with pellets being an important

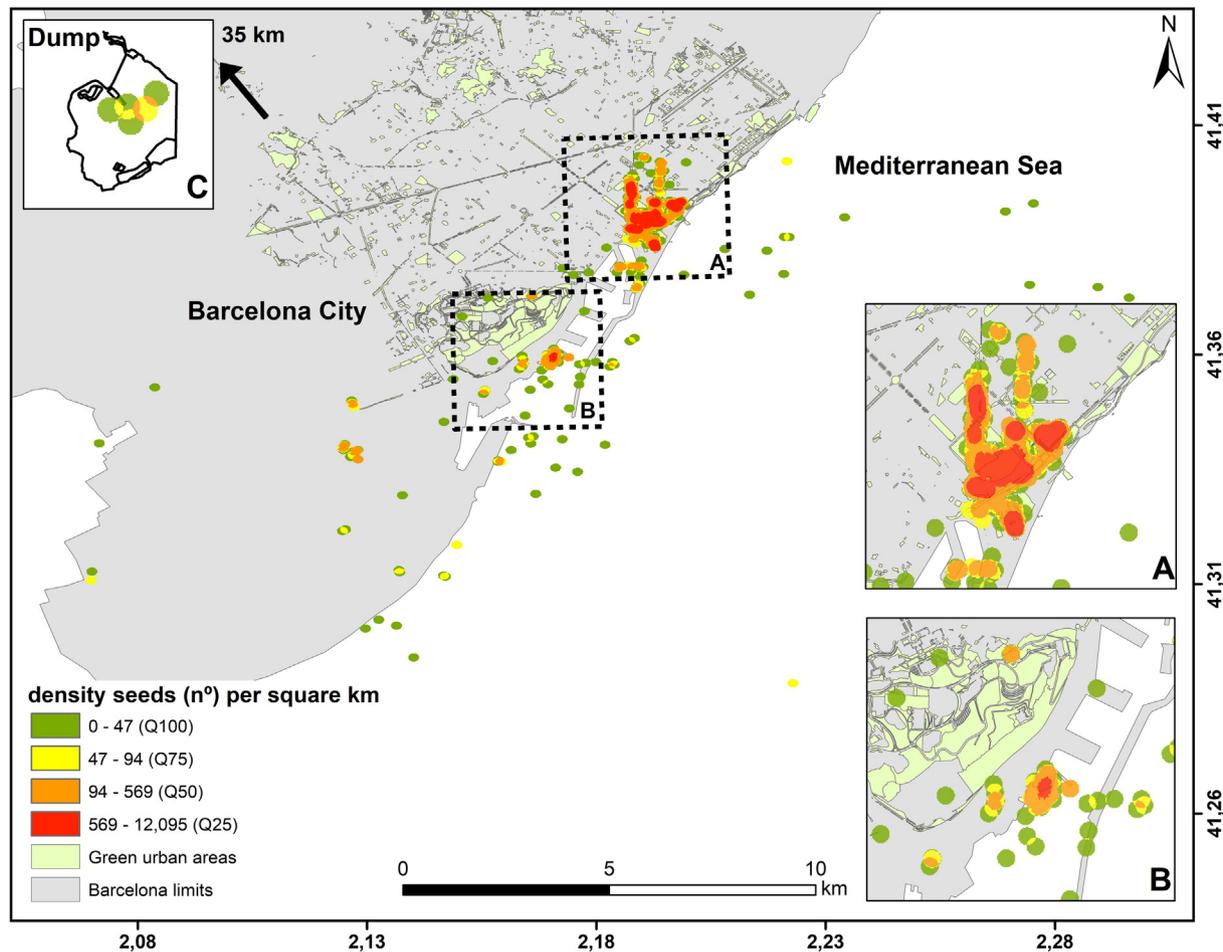


Fig. 4. Density of seeds dispersed based on a combined faecal and pellet deposition simulation models (1000 seeds each) and on the GPS trajectories of 20 yellow-legged gulls. Coloured areas show the estimated point density of seeds deposited, with red areas representing the highest seed densities and the 25% quantile, orange areas the 50% quantile and yellow areas the 75% quantile. Uncoloured areas reflect zero seed density. (A) Zoom-in of the highest density area within Barcelona city corresponding to Ciutadella Park. (B) Zoom-in of the Montjuïc urban hill park and Barcelona port. (C) Seeds deposited beyond Barcelona limits in a dump.

mechanism for seed dispersal (Padilla et al., 2012). In fact, gull chicks are fed by breeding gulls via pellets (Moreno et al., 2010), so the plant taxa list reported and the seed dispersal patterns generated from the pellet model may be more reliable.

The seed dispersal distance quantified by our models showed average dispersal distances of 770 m. The median dispersal distances (close to

Table 4

Habitat composition (in percentages) of the areas with higher densities of seeds dispersed by yellow-legged gulls in Barcelona city. Percentage of habitat types was calculated for 25% (Q25), 50% (Q50) and 75% (Q75) quantiles of seed deposition density maps, based on both faecal and pellet deposition. Note that quantiles are associated with colours from Fig. 4.

Density area	Q25%	Q50%	Q75%	All seeds
Suitable areas for seed establishment	33.14%	26.25%	23%	20.18%
Urban woodland	19.95	16.05	12.45	9.8
Grassland	3.3	0.9	1.6	3.37
Green urban area	9.88	9.3	8.95	7.01
Unsuitable areas for seed establishment	66.86%	73.75%	77%	79.82%
Other urban area	60.24	57.59	55.38	51.8
Port	6.62	15.54	18.73	23.34
Sea/beach	–	0.04	2.1	2.77
Waste dump	–	0.61	0.82	1.91
Total	100	100	100	100

100 m) reported here were lower than distances reported in previous spatial seed dispersal models parameterised with movement data of birds in natural environments. Kleyheeg et al. (2017) reported median dispersal distances for mallards *Anas platyrhynchos* between 600 and 3000 m, whereas Martín-Vélez et al. (2021b) reported dispersal distances for the lesser black-backed gull between 700 and 900 m with maximum dispersal distances greater than 150 km. The shorter seed dispersion distances found in our study may be due to the adaption of gulls to urban environments, where human refuse may provide predictable resources for chick rearing (Spelt et al., 2019) near the breeding places inside the city. Furthermore, gull mobility and distance travelled during breeding are lower than in the non-breeding period (Shamoun-Baranes et al., 2017; Ramírez et al., 2020). Future studies including non-breeding season will be necessary to understand the entire gull movements and thus, the complete seed dispersal shadows. Nevertheless, the importance of seed dispersion by gulls should not be underestimated. Several hundreds of seeds may be dispersed over distances exceeding 1 km on a daily basis by the yellow-legged gull population within and beyond Barcelona boundaries. Unlike random dispersal by wind or water, bird dispersal is more likely to transport many terrestrial seeds to locations that are favourable for germination.

Dispersal models estimated dispersal distances since other urban bird prey were consumed, but we have no information regarding the distance already travelled for primary dispersers. Total distance dispersal kernels should also take into account the movements of the primary consumers (Rogers et al., 2019). In this sense, dispersal distances modelled for gulls

may not reflect the entire dispersal distance of the plant species. Despite this, the gull's main prey, the pigeon, is a sedentary bird with little mobility and a home range of about 550 m, so that the total dispersal distance would not be greatly increased. On the other hand, maximum dispersal distances were associated with a nearby dump located about 35 km from Barcelona. Waste dumps are typical foraging habitats for gulls, so the possibility that gulls ingested seeds before flying to the dump is uncertain, and this may have overestimated the seed dispersal densities around the waste dump.

4.3. Seed dispersal across habitats and urban green planning

Urban areas are a mosaic of vegetation patches with varying degrees of connectivity embedded within a built environment matrix (Gelmi-Candusso and Hämäläinen, 2019). The majority of the seeds were deposited within the Barcelona city boundaries. Seeds outside Barcelona boundaries were deposited either at the waste dump or at the sea close to the port facilities. Seed deposition within Barcelona boundaries was expected given the dominance of gull trajectories within the city, which remained close to their nests and the Ciutadella park, near the area of capture. Due to the high mobility across the city, it is also expected that many seeds were deposited within urban areas that were not suitable for plant establishment. However, between 20 and 30% of the seeds are estimated to be deposited within green areas in Barcelona, including urban woodland, grasslands and green urban areas (e.g. parks), concentrated within the Ciutadella park and the surroundings of Montjuïc (Fig. 4A–B). Montjuïc is a mountain situated on the southwest of the city (3.6 km²). It is a main touristic hotspot with over 17 million visitors annually. Moreover, it is partly surrounded by a railway, expressway, and is next to the seaport.

Many initiatives in different cities aim to increase and manage urban parks, gardens and nature reserves to facilitate biodiversity conservation and promote landscape connectivity (Horta et al., 2018; Pla Natura, 2021–2030). At a time of unprecedented environmental change, including ongoing biodiversity loss, urban landscapes need to reflect local environmental conditions to preserve the future of the natural environment. Barcelona is a reference city which has developed a green plan to enhance urban biodiversity by promoting and protecting native plant species and enhancing green connectivity by creating a green areas network (Ajuntament de Barcelona, 2013; Parés et al., 2016). National and European directives and The Territorial Metropolitan Plan of Barcelona (TMPB) aim to include biodiversity conservation and the improvement of ecosystem services in urban planning and in the design of green infrastructure (Basnou et al., 2020). Future Barcelona nature plan directives for 2021–2030 involve the conservation of natural heritage by preventing species and habitat loss, enhancing green connectivity and creating a more resilient city to face climate change, among other efforts (Pla Natura, 2021–2030).

In this study, seven plant taxa (*Ficus carica*, *Echinochloa crus-galli*, *Solanum chenopodioides*, *Solanum eleagnifolium*, *Actinia deliciosa*, *Washingtonia robusta*, *Cuscuta cf. campestris*) were non-native to Spain (Aymerich and Sáez, 2019). *Echinochloa crus-galli* is an important weed species in agricultural landscapes, with adaptive characteristics to survive and over compete other plant species (Bajwa et al., 2015). *Solanum eleagnifolium* is considered one of the worse alien plant species within Europe due to its capacity for spreading and establishment, and previously assumed to be dispersed by abiotic means (Vladimirov et al., 2015). Therefore, seed dispersal between green urban areas by gulls may become a “disservice” if those alien plant species are transported (Wenny et al., 2016), interfering with urban plans to promote native flora within urban environments. If alien species dominate in urban areas, the gulls have the potential to disperse their seeds to natural and rural areas in the neighbourhood of the cities. City managers should consider that non-native plants used in urban green patches may be dispersed by birds, another reason to favour native vegetation over non-native species in urban planning. Special attention should be paid to Ciutadella Park and its surroundings, as a higher density of seeds is expected to be deposited via yellow-legged gulls in this area.

5. Conclusions

Urban yellow-legged gulls may play an unrecognized role in the seed dispersal of both plants with fleshy fruit through primary dispersal and plants lacking fleshy fruit via secondary dispersal by granivorous bird consumption. The seed shadows predicted from seed retention curves and gull movements indicate that gulls can disperse around 20–30% of seeds between green urban areas. Seven of the plants dispersed are considered alien species, and gulls may increase the risk of dispersal of these alien species. Urban planning for Barcelona is based on native plant species, and special attention should be paid to alien plants dispersed by birds, which could pose a risk to natural habitats in urban ecosystems.

CRedit authorship contribution statement

VMV wrote the first draft of the manuscript and performed data analyses; TM collected the field data and reviewed the manuscript; IF contributed to designing the methodology, contributed to data interpretation and reviewed the manuscript several times; ASM collected the laboratory data; RA collected the field data; JF contributed to problem conceptualization, methodology and to improving the manuscript; ALK identified the plant taxa and reviewed the manuscript; JN conceived the idea, contributed to methodology design and reviewed the manuscript several times.

Availability of data

Data will be uploaded to CSIC repository.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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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.2022.153535>.

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