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Spatial patterns of weed dispersal by wintering gulls within and beyond an agricultural landscape

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Abstract

1. Non-frugivorous waterbirds disperse a wide variety of plants by endozoochory, providing longer-dispersal distances than other mechanisms. Many waterbirds visit both agricultural and natural landscapes during their daily movements, but potential bird-mediated dispersal of weed plants within and from agricultural landscapes to other habitats is commonly overlooked. Gulls (Laridae) are expanding in numbers and increasingly exploiting anthropogenic habitats worldwide, with possible growing implications for the spread of weeds. Yet, to date, there are no studies on the spatial distribution of weed dispersal by waterbirds.
2. We developed a plant dispersal model based on movements of 19 *Larus fuscus* using ricefields, via GPS telemetry. We combined daily movements with two curves estimating the retention times of plant seeds in their guts: (a) an experimental curve based on retention time in captivity for four weeds with dry fruits known to be dispersed by gulls: *Juncus bufonius*, *Cyperus difformis*, *Polypogon monspeliensis* and the alien *Amaranthus retroflexus*; (b) a theoretical curve based on the interspecific scaling relationship between body mass and mean retention time.
3. Median dispersal distances of weed plant seeds by gulls ranged between 690 and 940 m, but maximum distances exceeded 150 km. The theoretical retention time model showed higher median dispersal distances than the experimental retention time model. Spatial patterns of weed deposition were very similar between retention time methods, and most strongly depended on gull movements. Variation between individual gulls had little influence on seed shadows. About 92% of all seeds (>10,000 intact seeds per day) were dispersed within the ricefield area of 370 km². The remaining 8% of seeds were deposited beyond ricefields into other habitats, 42% of which reached moist environments (other irrigated agriculture, rivers and natural wetlands) presumably suitable for weed establishment.

4. *Synthesis.* Gulls can disperse weed plants over long distances across a mosaic of habitats. This implies exchange of weed plant species between human-dominated and natural areas by waterbirds as dispersal vectors. This spatial study highlights the importance of non-frugivorous birds for long-distance plant dispersal, which is generally an overlooked mechanism in studies aiming to predict and manage expansion of weed plants.

KEYWORDS

GPS data, gut retention time, *Larus fuscus*, long-distance dispersal, movement ecology, ricefields

1 | INTRODUCTION

Seed dispersal plays a central role in the meta-population dynamics and long-term persistence of plant species (Willson & Traveset, 2000). Plant seed dispersal is of particular interest for weeds (i.e. plants that spontaneously grow on land modified by humans; Bourgeois et al., 2019), because many weeds cause high economic cost to agriculture and many are invasive species with severe ecological and societal impact. For example, estimated costs and yield loss due to weed management in Australia exceeded USD 1,000 million in 2002 (Sinden et al., 2004). Nevertheless, we know little about the role of birds that use anthropogenic (e.g. agricultural) habitats in weed dispersal.

Dispersal via gut passage (endozoochory) is ideal for long-distance seed dispersal, but it has been widely, yet erroneously, assumed that this mechanism is limited to frugivorous animals (i.e. those feeding on fleshy fruits; Costea et al., 2019). Only plants with a fleshy fruit are assigned to an 'endozoochory syndrome' used to predict dispersal mechanisms, and only 8% of the European flora and 1.5% of agricultural weeds worldwide have such a syndrome, compared to 63% and 80%, respectively, for an unspecialized syndrome or 'barochory' (Benvenuti, 2007; Heleno & Vargas, 2015). Therefore, syndromes imply that animals are of little importance for the dispersal of weeds. On the other hand, empirical data demonstrate that seeds dispersed by animals tend to be dispersed further than seeds dispersed by abiotic mechanisms, including wind (Bullock et al., 2017; Vittoz & Engler, 2007). Hence, weed dispersal by animals may have relatively greater impact than previously thought.

Recent studies have demonstrated that granivorous and omnivorous waterbirds such as ducks or gulls disperse a high diversity and abundance of seeds from angiosperms with a non-fleshy fruit (NFF from hereon) by endozoochory, including many agricultural weeds (Farmer et al., 2017; Lovas-Kiss, Sánchez, et al., 2018; Lovas-Kiss, Vizi, et al., 2018; Soons et al., 2016). NFF seeds dispersed by waterbird endozoochory seem to be just as adapted to survive gut passage as those from fleshy-fruited plants (Costea et al., 2019). Fixation on morphological syndromes leads to the systematic overlooking of endozoochory for weeds by non-frugivorous birds that likely disperse seeds over great distances. Especially in human-modified

landscapes, we can expect that endozoochory of weeds by waterbirds will greatly increase the probability of seeds dispersing out of a given agricultural field, beyond adjacent fields, and into other habitats including other crops. Understanding and controlling the spread of weeds between fields is particularly important, because even a single herbicide-resistant plant colonizing a field can lead to a total field infestation. For example, Palmer Amaranth *Amaranthus palmeri* took over cotton fields within 3 years (Norsworthy et al., 2014).

Spatial modelling of plant dispersal is a major research tool in plant ecology because of its importance in predicting plant distribution and population dynamics (Husband & Barret, 1996; Jeltsch et al., 2008), as well as for implementing effective management strategies (Aben et al., 2016). In recent decades, data have been collected on the retention time of seeds in the avian digestive system, both for frugivores and waterbirds (Lovas-Kiss et al., 2020), to estimate potential dispersal distances. Experimental retention time data have been combined with animal movement data in mechanistic models that estimate seed dispersal distances. However, most models to date focused on dispersal by frugivorous birds (Côtés & Uriarte, 2013; Godínez-Alvarez et al., 2020), and few studies have applied this approach to questions about dispersal of seeds by non-frugivorous birds (Kleyheeg et al., 2017). Moreover, the chances of plant establishment following seed dispersal depend critically on the spatial endpoints (i.e. into what habitats seeds are deposited), which have also been understudied.

Methodologically, most previous studies of waterbird endozoochory have estimated dispersal distances simply by multiplying mean retention times by the average flight speed, bypassing a need for empirical movement data (Farmer et al., 2017; Nogales et al., 2001; Raulings et al., 2011). This likely overestimates seed dispersal distances, and new technology using GPS tracking devices can reduce uncertainty of bird movements involved in seed dispersal compared to radio-tracking studies (e.g. Bartel et al., 2018). High-resolution data allow the creation of more reliable mechanistic models in which the speed, direction and duration of bird movements are not fixed parameters, and individual variation in movement patterns can be taken into account.

Understanding the role that waterbirds play in the dispersal and spatial dynamics of weeds will help to predict their spread and

to develop new management strategies in agricultural landscapes. Here, we aimed to assess the importance of non-frugivorous bird movements for the dispersal of weeds throughout a human-modified landscape. We present a case study centred on Doñana ricefields, Spain's largest rice-growing area where many waterbirds (e.g. gulls) feed during harvesting. The lesser black-backed gull *Larus fuscus* has been increasing in the ricefields (Rendón et al., 2008) and it is known to disperse at least 15 different plants while feeding there (Lovas-Kiss, Sánchez, et al., 2018; Martín-Vélez et al., 2021; Table S1). Furthermore, recent movement studies showed the importance of the ricefields for *L. fuscus* during the non-breeding season (Martín-Vélez et al., 2020). Using GPS data on *L. fuscus* movements, we model their potential to disperse NFF weeds between different rice fields, as well as beyond the ricefields into other anthropogenic and natural habitats. The weeds considered in this study impact ricefields as well as other crops in the same region (e.g. cotton, wheat, vineyards).

The specific objective of this study is to determine the extent to which gulls disperse weeds over distances that exceed field boundaries by quantifying seed dispersal distances, spatial seed shadows and the habitat types into which seeds are deposited. To address this objective, we modelled seed dispersal based on two different seed retention time curves: an experimentally assessed curve based on data from captive gulls, and a theoretically assessed curve based on the known scaling relationship between body mass and gut retention times of birds.

2 | MATERIALS AND METHODS

2.1 | Study area and species

The ricefields (37,000 ha) in the Guadalquivir marshes in Andalusia account for up to 42% of the total rice production in Spain. They are located in the surroundings of Doñana National Park and World Heritage Site, and are part of one of the most important wetland complexes for waterbirds in the Western Palearctic (Green et al., 2018; Rendón et al., 2008). These ricefields provide important habitat for many wintering waterbirds that use them both for feeding and roosting, especially during and just after the rice harvest (Rendón et al., 2008; Toral & Figueroa, 2010).

The lesser black-backed gull *L. fuscus* is migratory, breeds in Northern Europe (Baert et al., 2018) and winters in Southern Europe. Due to its opportunistic and generalist diet, *L. fuscus* has largely switched from marine to inland habitats to exploit resources of anthropogenic origin such as ricefields and landfills (Ramos et al., 2009), and is now the second most numerous wintering waterbird in Andalusian wetlands, with a population of over 80,000 (Martín-Vélez et al., 2020). Up to 15,000 gulls are regularly counted in the ricefields west of the Guadalquivir river (the only ones covered in aerial counts), with peaks in early winter during the harvest (Rendón et al., 2008). The ricefields are the most important node in the network of sites used by *L. fuscus* in Andalusia (Martín-Vélez et al., 2021). This network shows high functional connectivity

between different habitat types (Martín-Vélez et al., 2020), increasing the potential of *L. fuscus* as vectors for seeds, including those of agricultural weeds. During the harvest, *L. fuscus* feed mainly on alien red swamp crayfish *Procambarus clarkii* exposed as the rice is harvested, and they disperse seeds carried on the outside of the crayfish, or ingested while feeding on rice grains (Lovas-Kiss, Sánchez, et al., 2018; Martín-Vélez et al., 2021). Gulls concentrate their feeding during the day on fields where harvesting or disking is underway, later moving to dykes and other roosting sites.

2.2 | Gull tracking data

A large number of gulls have been equipped with Global Positioning System (GPS) trackers, as part of the University of Amsterdam Bird Tracking System (UvA-BiTS; Baert et al., 2018; Shamoun-Baranes et al., 2017; Thaxter et al., 2015), stored in a centralized database (<http://www.uva-bits.nl>; Bouten et al., 2013). For this study, we first extracted all data points within the rectangle created between latitudes of 36.0°–40.5°N and longitudes of 0.0°–9.0°W (i.e. the whole of Andalusia) between September and December from 2010 to 2017. These months cover the harvesting period when gulls feed within the ricefields, although fields often remain flooded for some weeks in January, when they may be used as roost sites for gulls feeding in landfills (Martín-Vélez et al., 2020).

For our analysis, we used the following parameters recorded by the GPS loggers: body mass, date, time of the day (UTC), latitude, longitude and instantaneous speed. Position accuracy for a stationary logger transmitting a signal every 10 min was on average 30 m (range 9–108 m; Bouten et al., 2013). 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 10 and 60 min) and trajectory speed (km/hr). We filtered the dataset for quality by deleting any fix with a trajectory speed greater than 80 km/hr, which is the realistic limit for bird flight speeds (Klaassen et al., 2012). We also deleted gaps in the trajectories of greater than 120 min and assumed they were due to low battery power.

We selected all GPS points within the Doñana ricefields based on the CORINE Land Cover (CLC) 2012 habitat type (Coordination of Information on the Environment, CLC; <https://land.copernicus.eu/>). CLC database is a land cover map (scale 1:100,000) generated by EU countries following the same methodology. Based on the speed histogram within the ricefields, we classified the data as either 'stationary' or 'active flight', taking 13 km/hr (i.e. 3.6 m/s) as the threshold (Figure S1). We assumed 'active flight' represented displacements of gulls between foraging or roosting sites that are relevant for seed dispersal, and that no seed ingestion occurred during the night because gulls are diurnal foragers. We further assumed that seed ingestion occurred within ricefields between 07:00 and 17:00 hr UTC according to the timing of 'active flight' (Figure S2). This time range excluded the main roosting periods (especially night time) when seed ingestion is improbable (see also

Martín-Vélez et al., 2019 for diel rhythms of *L. fuscus*). The GPS points within the ricefields correspond to a total of 1,867 gull-days, from a combination of eight different winters from 2010 to 2017 and 19 different individual gulls from five different breeding colonies (eight individuals from Zeebrugge, Belgium; five from Texel, the Netherlands; three from Skokholm and three from Walney, UK). Up to eight individuals with GPS trackers were present in a given winter, and each individual was present for between one and four winters.

To calculate the probability distribution of seed dispersal events according to dispersal distance (i.e. the 'dispersal kernel', Nathan et al., 2012), data on retention times of seeds in the digestive system are required. To estimate the time elapsed between seed ingestion and excretion, we used both experimental and theoretical approaches. Feeding experiments using captive waterbirds have provided valuable information on factors influencing gut retention times, such as seed size and hardness, or diet (e.g. Charalambidou et al., 2005; van Leeuwen, Van Der Velde, et al., 2012; Lovas-Kiss et al., 2020), but it is unclear to what extent results from captivity (where birds are in cages) represent retention times under natural conditions (with actively moving birds), given the influence of activity on digestion (van Leeuwen, Tollenaar, et al., 2012). We therefore assessed retention times experimentally, but compared our results with a theoretical retention time curve based on body mass.

2.3 | Experimental seed retention time

A seed retention curve was calculated from an experiment carried out in January 2020 with seven captive *L. fuscus* individuals as part of a related study (A. Ansotegui, F. Hortas, V. Martín-Vélez, A.J. Green, M.J. Navarro, J.M. Peralta-Sanchez, S. Redón, & M.I. Sánchez, in prep.). Individuals were captured during January 2020 near Seville, Spain. For this study, we used data for four dry-fruited weed species (200 seeds each per gull of toad rush *Juncus bufonius*, small-flowered nut sedge *Cyperus difformis*, annual beard grass *Polypogon monspeliensis* and common amaranth *Amaranthus retroflexus*; a combined total of 5,600 seeds for all gull individuals). These weeds are associated with rice crops and are four of the 15 angiosperm species known to be dispersed by *L. fuscus* in the study area (Table S1). *Cyperus difformis* is strongly associated with rice and is considered one of the world's 40 worst weeds (Bryson & Carter, 2008). The other weeds inhabit a broad range of disturbed habitats and crops (AgroAtlas, 2020), for example, *J. bufonius* is a weed of wheat and barley (Broster et al., 2012). Herbicide resistance has been recorded for all but *J. bufonius* (Heap, 2020). *Juncus bufonius* and *A. retroflexus* are considered noxious weeds by Bourgeois et al. (2019), and the latter is alien to Spain.

To facilitate feeding, the seeds were mixed with a bread pellet of about 2 cm diameter and fed to the gulls. Gulls were fed with sardines ad libitum for the duration of the experiment. After seed ingestion, faecal samples were collected in time intervals: first after half an hour, then every hour until the first 6 hr, then every 2 hr from 6 to

12 hr, and then every 4 hr until 34 hr (the end of the experiment). In the laboratory, faeces were sieved through a 40- μ m mesh and intact seeds were separated and counted. To generate the retention time curve (Figure 1a), we assumed the retention time of any recovered seed was the midpoint between collection times (e.g. if a seed came from faeces collected at 2.5 hr and the previous collection was at 1.5 hr, we assigned a retention time of 2 hr). Seed retention times have been overestimated during previous captive studies by assuming that they correspond to the timing of faecal collection (i.e. 2.5 hr in the above case). The retention curve was generated as kernel density estimates with the *density* function (bandwidth = 1) of the *STATS* package in R.

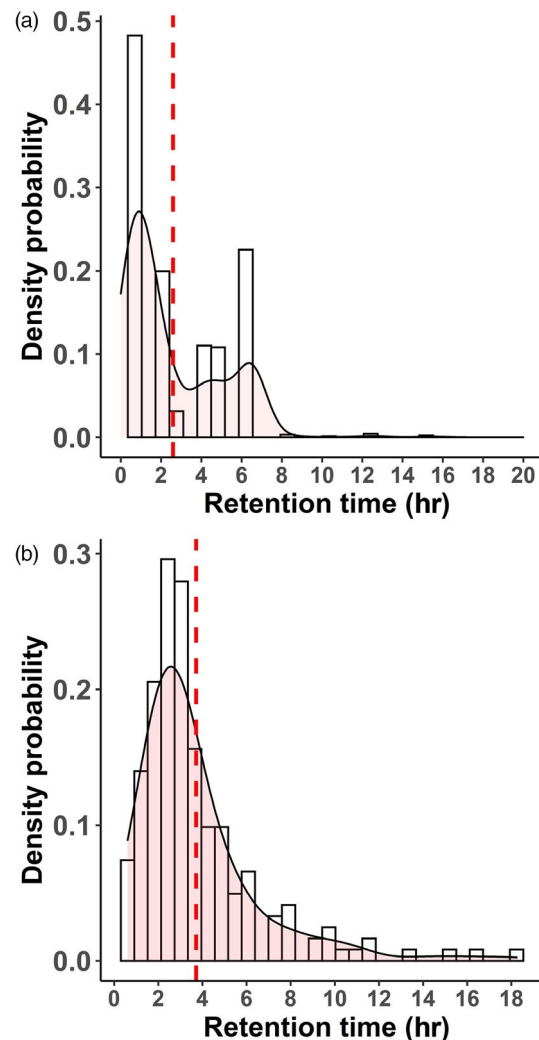


FIGURE 1 (a) Experimental retention time curve (density probability on y-axis and retention time in hours on x-axis, bandwidth = 1) generated from 4,465 seeds recovered from four plant taxa used in a captive experiment. (b) Theoretical curve derived from random sampling ($N = 100$) based on 3.1 hr mean retention time (calculated from Equation 1) and a lognormal curve with $\text{sdlog} = 0.7$ corresponding to the shape of the curve (after Viana et al., 2016). Red dashed lines indicate mean retention times in both curves: 2.6 in the experimental curve and 3.7 from the random generation (with shape 0.7) in the theoretical curve

2.4 | Theoretical seed retention time

We tested the robustness of our final results and the importance of the retention time distribution in the seed dispersal model using a theoretical retention time curve (Figure 1b). We estimated a curve based on an allometric equation (Equation 1) relating mean retention time to body mass across bird species (Yoshikawa et al., 2019). Using a mean body mass of 845 ± 127 SD g (from the 19 gulls we tracked), this equation gives a mean retention time of 3.1 hr (Equation 1). Following Viana et al. (2016), we then generated a lognormal retention time distribution from a shape (sdlog) and a scaling (meanlog) parameter. The scaling parameter is calculated from the mean retention time of 3.1 hr, and the shape parameter is fixed at 0.7 (randomly generated using the *rlnorm* function in R), as proposed by Viana et al. (2016) for endozoochory relationships (Figure 1).

$$\text{Log}_{10} \text{ mean seed retention time (min)} \\ = 0.631 (\pm 0.148 \text{ SE}) + 0.561 (\pm 0.063 \text{ SE}) * \log_{10} (\text{body mass g}). \quad (1)$$

2.5 | Seed deposition modelling

We randomly selected one of the 1,867 gull-days and assumed that a seed was ingested at a time t_0 randomly assigned to a point between 07:00 hr and 17:00 hr. Based on the experimental or the theoretical retention time curve, we randomly selected a retention time t_1 when the seed would be egested, based on the density probability from the 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 point at t_1 , and the distance the seed was dispersed was calculated based on the Euclidean distance between GPS points at t_0 and t_1 . We repeated such randomizations 10,000 times for each of the experimental and theoretical models. Thus, each simulation represented the dispersal of 10,000 seeds in the study area. The mean number of intact seeds per *L. fuscus* faecal sample in the field is approximately 1, and around a fifth of these seeds germinate in the laboratory (Lovas-Kiss, Sánchez, et al., 2018; Martín-Velez et al., 2021). Each faecal sample represents only 12.5% of total daily faecal output per bird (Hahn et al., 2007),

and the number of gulls in the ricefields exceeds 15,000 (Rendón et al., 2008). Therefore, each simulation represented only a fraction (roughly 40%) of the number of viable seed dispersal events by *L. fuscus* in a typical day.

To test for model sensitivity and robustness in trajectory movements, we ran the model again after removing the two of the 19 individuals with the longest geometric mean seed dispersal distances, according to model outputs. We then removed sequentially the four, six and eight individuals with the longest mean dispersal distances. This enabled us to assess the influence of variation in trajectories between individuals (which also represented different years) on the cumulative frequency distributions of the dispersal distance curves. To test further for individual variation, we also took the eight individuals that occurred within the same winter (2016) and ran independent models for each individual to compare resulting dispersal distances.

We summarized dispersal distances using geometric means instead of arithmetic means because their distribution was strongly right-skewed. However, these geometric means were consistently lower than the medians (Table 1). For spatial model visualization, we first projected the seed point coordinates to UTM and applied the *Point Density* tool in Arc Map 10.4 which calculates a magnitude-per-unit area from point features that fall within a neighbourhood around each cell. We applied a cell size of 100 m and a search radius for neighbouring cells of 1 km. We set up the output values based on standard deviations as default to visualize the densities measured as number of seeds km^{-2} . Furthermore, we overlapped the seeds deposited outside of the ricefields with a regional land use shapefile (Junta de Andalucía, 2013) with more detailed land uses than Corine Land Cover. This allowed us to determine the main habitat types into which seeds were dispersed. The six main habitat categories were as follows: river Guadalquivir, other water bodies (e.g. lakes or reservoirs), natural vegetation, urban, permanent irrigated agriculture and other agriculture (details in Table S3). As three of the weeds used for the study require moist soils (with high Ellenberg moisture values, Table S1), habitats closely associated with water (e.g. other irrigated agriculture, river, waterbodies; Table S3) were considered suitable for weed deposition.

TABLE 1 Comparison between models with experimental and theoretical retention time curves, presenting numbers of deposited seeds and dispersal distances (in km, geometric means, quantiles and maximum distances). Results are given for all seeds combined (total), seeds deposited within ricefields, and seeds deposited outside of ricefields (percentages in brackets). Note 50% quantiles are the medians, and arithmetic means would be considerably higher (e.g. 3.51 km for Experimental total and 4.2 km for Theoretical total)

Model	No. deposited seeds	Dispersal distance (km)				
		Geometric mean (95% CI)	25%	50%	75%	Max
Experimental						
Total	10,000	0.58 (0.56–0.60)	0.16	0.69	2.33	150.96
Within	9,277 (92.77%)	0.45 (0.43–0.47)	0.14	0.57	1.81	36.96
Outside	723 (7.2%)	14.30 (12.95–15.80)	8.25	17.88	41.82	150.96
Theoretical						
Total	10,000	0.87 (0.84–0.90)	0.27	0.94	2.88	243.00
Within	9,186 (91.86%)	0.67 (0.65–0.70)	0.23	0.78	2.21	39.77
Outside	814 (8.14%)	16.30 (14.98–17.75)	9.66	19.03	42.99	243.00

3 | RESULTS

3.1 | Experimental seed retention times

There were no significant differences in the retention times among seed species (Kruskal–Wallis chi-squared = 2.77, $df = 3$, $p = 0.429$). We therefore summed all seed species to generate an overall retention time curve, based on a total of 4,465 intact seeds recovered from the seven individual gulls used in the captive experiment (Figure 1a). Mean retention time was 2.6 hr and the last seeds were recovered after 29 hr.

3.2 | Model based on experimental retention times

The geometric mean dispersal distance of 10,000 seeds from randomizations based on experimental retention times was 0.58 km

(Table 1). More than 7% (723) of the seeds were dispersed outside of the ricefields (see white dots in Figure 2). Geometric mean dispersal distance for seeds egested within ricefields was 0.45 km with a maximum of 36.7 km, compared to a geometric mean of 14.3 km and maximum of 151 km for seeds egested outside of ricefields (Table 1).

There were statistically significant differences in the dispersal distances recorded between the 19 gull individuals whose movements were tracked (Kruskal–Wallis chi-squared = 283.98, $df = 18$, $p < 0.001$) and dispersal kernels varied depending on the individual selected for the model, even within a given winter (Figure S3; Table S2). However, sensitivity analyses for robustness showed no consistent reductions in mean seed dispersal distances when those pairs of gull individuals with longest geometric mean dispersal distances were removed sequentially from the model (Table S3). Of the 19 individuals, three had a maximum seed dispersal distance exceeding 100 km.

Areas with the highest densities of deposited seeds (up to 194 seeds km^{-2}) were restricted to the ricefield area (Figure 2). Seeds

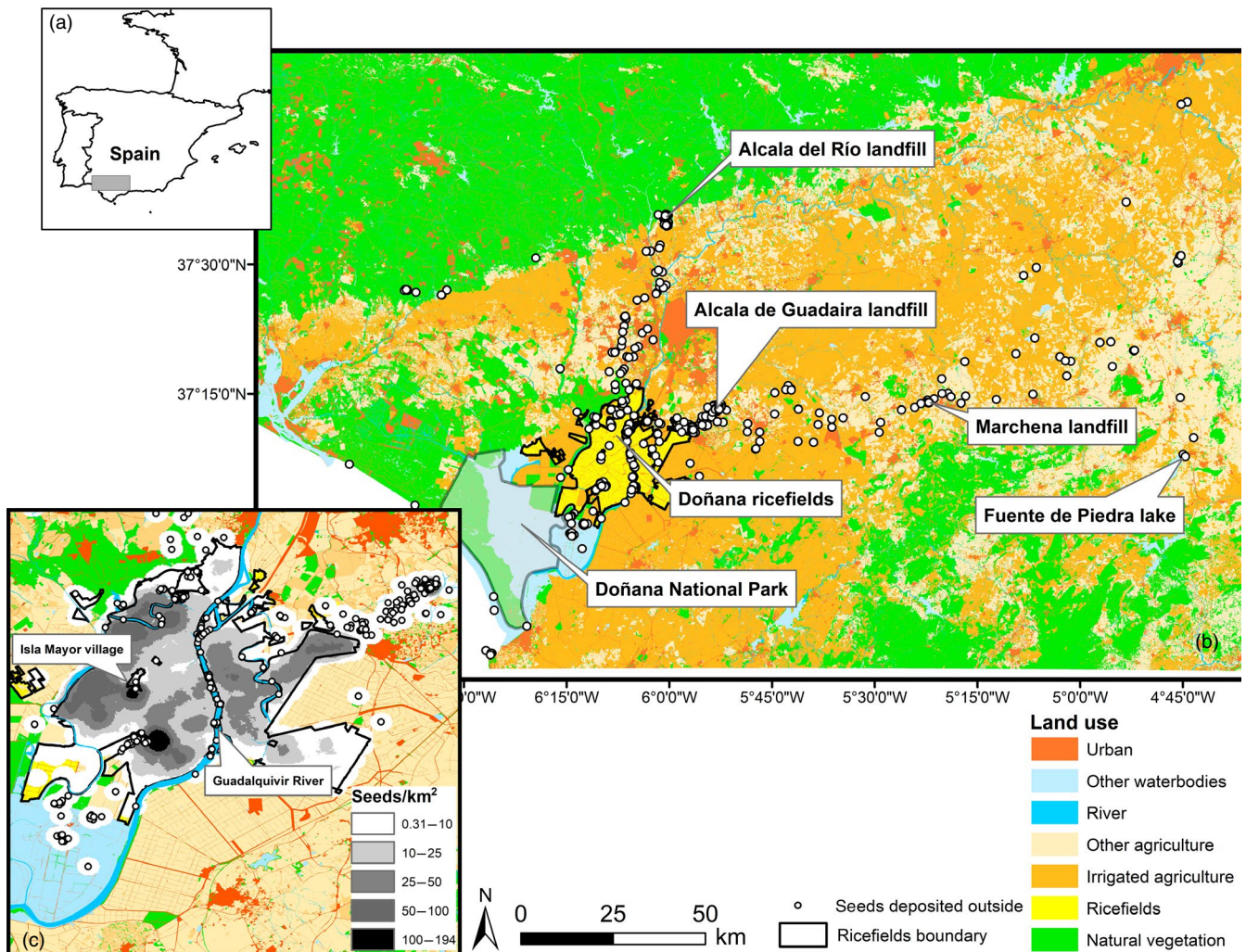


FIGURE 2 Dispersal for 10,000 seeds modelled with an experimental retention time curve and GPS trajectories of 19 gulls. (a) Location of the study area in Spain. (b) Seeds deposited outside ricefields (723 from the total of 10,000 seeds) shown as white dots. Coloured land use shows seven categories extracted from Junta de Andalucía (2013). (c) Estimated point density of seeds deposited within ricefields, classified into five categories. Darker areas indicate higher densities of seeds (maximum 194 km^{-2} , minimum 0.13 km^{-2}). Yellow areas reflect zero seed density

egested outside the ricefield landscape were deposited mainly in urban habitats (average density of 39 seeds km^{-2} ; Table S4) that are less likely to be suitable for these weed species, including three solid waste treatment plants/landfills (Figure 2). However, other seeds were deposited in agricultural lands, including permanently irrigated lands (average density 14.7 seeds km^{-2}), and other agricultural lands (3.7 seeds km^{-2} , Table S4) such as olive groves and vineyards. Some seeds (14.3 seeds km^{-2}) were dispersed within the stretch of the Guadalquivir river that runs through the middle of the ricefield area (Figure 2). 10.7 seeds km^{-2} were deposited in areas of natural vegetation such as grasslands or oak woodlands. Finally, a fraction of seeds (4.6 seeds km^{-2}) was deposited in other waterbodies, including protected areas such as the nearby Doñana Natural Space, and Fuente de Piedra Lake situated at 118 km from

the nearest ricefield (Figure 2). Around 42% of the seeds egested outside the ricefields were deposited in an environment with high water availability that is most likely to enable weeds to establish (Table S4).

3.3 | Model based on theoretical retention times

Geometric mean dispersal distance from the model based on a theoretical retention time curve was 0.87 km, 33% more than for the experimental model (Table 1). This shift is in line with the greater mean retention time in the theoretical curve (Figure 1). The theoretical model predicted significantly longer-dispersal distances than the experimental model (Wilcoxon signed-rank test, $W = 44,932,211$, $p < 0.0001$). Cumulative frequency distributions showed that the seed dispersal distances predicted by the two models diverged considerably for distances of <1 km, but then converged at greater distances (Figure 3a, see also Table 1).

According to the theoretical model, over 8% (814) of seeds were deposited outside of the ricefields (Table 1). Dispersal distances for seeds moved outside the ricefields were only slightly higher in general than for the experimental model (Table 1, Figure 3b), but the maximum dispersal distance (243 km) was much higher. The highest densities within the ricefields (194 seeds km^{-2}) and spatial seed deposition patterns were similar to those found using experimental retention times (Figure S4).

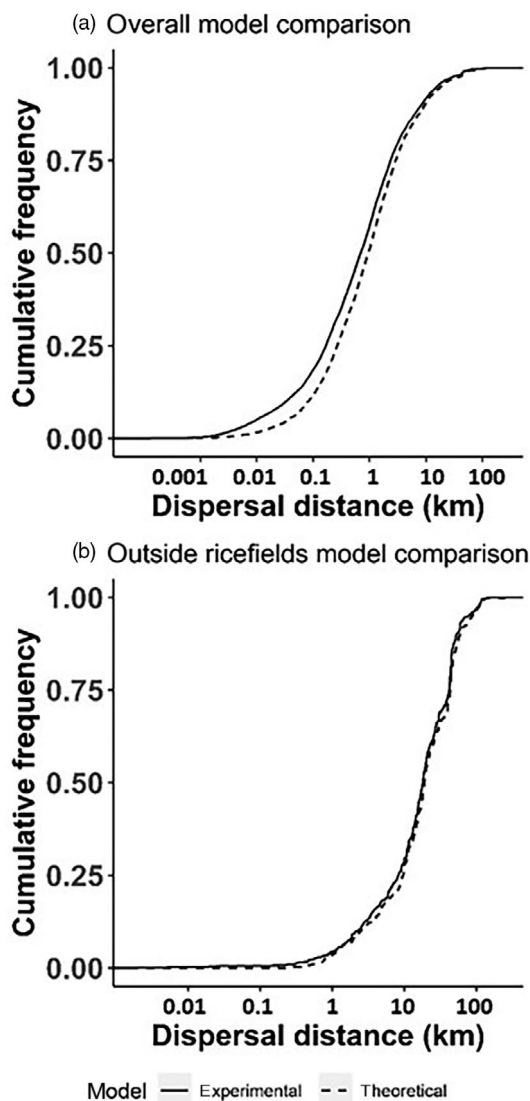


FIGURE 3 Cumulative frequency distributions of dispersal distances (km) obtained from models using experimental (solid line) and theoretical (dashed line) retention times, with a log scale on the X-axis. (a) Based on all 10,000 seeds modelled. (b) Only for seeds deposited outside ricefields (723 seeds for experimental and 814 for theoretical models)

4 | DISCUSSION

We compared experimental and theoretical models with different retention time curves, and found significant differences in seed dispersal distances for *L. fuscus*. We quantified seed shadows, and found that several thousand weed seeds are dispersed over distances exceeding 2 km on a daily basis by the *L. fuscus* population, this being just one of the waterbird species frequenting the ricefields. *Larus fuscus* often disperse weeds from ricefields into other suitable habitats.

All plant species used in this study were NFF weeds previously recorded in *L. fuscus* excreta from the ricefields (Lovas-Kiss, Sánchez, et al., 2018; Martín-Vélez et al., 2021). The probability of weed establishment depends on the suitability of the microhabitat where the seed is deposited, and germinability. Around 20% of seeds from *L. fuscus* excreta collected in ricefields later germinated in the laboratory, although germinability was reduced by the delay between sample collection and germination tests (Lovas-Kiss, Sánchez, et al., 2018; Martín-Vélez et al., 2021). The number of seeds dispersed in our models is less than the number expected during a single day in the ricefields, given the numbers of gulls present and their rates of seed egestion (see Section 2).

Our study of seed dispersal by waterbirds combines high-resolution movement data in the landscape with local information on what plant taxa are actually dispersed by endozoochory. Kleyheeg et al. (2017)

modelled seed dispersal by mallards using similar high-resolution GPS data, and reported seed dispersal distances of 0.6–3 km. We found a high frequency of seed dispersal distances of >3 km in *L. fuscus* because they regularly shifted their roosting places in a dynamic response to the rice harvest cycle (Martín-Vélez et al., 2020), whereas wintering mallards often remain within a limited home range for many weeks at a time (Kleyheeg et al., 2017; Sauter et al., 2012).

Our results based on GPS data confirm that previous studies assuming a straight, continuous flight (e.g. Farmer et al., 2017; Nogales et al., 2001) overestimate the seed dispersal distances for waterbird vectors. Based on the maximum retention time from the experimental curve (27.5 hr) and an average flight speed of about 40 km/hr (Klaassen et al., 2012), seeds would be expected to cover far greater distances of up to 1,000 km. This is unrealistic, partly because birds generally roost at night, even during seasonal migrations between breeding and wintering grounds, when *L. fuscus* make many stopovers (Klaassen et al., 2012; Shamoun-Baranes et al., 2017).

4.1 | Importance of avian vectors for weeds

The dispersal distances obtained in our results underline the importance of avian endozoochory for NFF plants when compared to the dispersal distances expected for abiotic mechanisms, including wind. Tamme et al. (2014) suggested that *J. bufonius* had a maximum dispersal distance (MDD) via wind of only 100 m, which is exceeded by over 75% of seeds dispersed by *L. fuscus* (Table 1). *Juncus bufonius* is the dominant seed in *L. fuscus* excreta from ricefields (Lovas-Kiss, Sánchez, et al., 2018; Martín-Vélez et al., 2021), and we found MDDs over 100 km, that is, >10³ greater than the MDD expected by wind. Similarly, Dauer et al. (2006) estimated the wind dispersal distances of the horseweed *Conyza canadensis* (present in our study area; Martín-Vélez et al., 2021) as between 30 and 100 m. *Cyperus difformis* has been assigned to a barochory syndrome, and our other study weeds to an epizoochory syndrome (Table S1; Julve, 1998). Epizoochory by waterbirds is much rarer than endozoochory (Green et al., 2016). Rodents are the only mammals abundant in ricefields, and epizoochory by them or by crayfish is unlikely to provide dispersal distances that approach those provided by waterbirds. Human vectors are hugely important for long-distance dispersal of weeds, especially between different fields managed by the same people or otherwise strongly connected by human movements (Benvenuti, 2007). However, the seed shadows generated by avian and human vectors, and the habitats they are dispersed into, are likely to differ greatly.

Seed dispersal distances for gull endozoochory also generally exceed those recorded for frugivorous birds, which are mainly <200 m with maxima of 1.5–14.5 km in most cases, although these are still longer-dispersal distances than from abiotic mechanisms (Bullock et al., 2017; Wenny et al., 2016). Other waterbirds, such as storks or egrets, feed on crayfish and rice in the ricefields in a similar manner to *L. fuscus*, and are certain to increase the rates of weed dispersal. The relative abundance of different weed species dispersed by White storks *Ciconia ciconia* is the same as for *L. fuscus*

(Martín-Vélez et al., 2021). However, seed shadows likely differ for each waterbird species as they have different movement patterns. The weeds included in our models are also likely to be dispersed by wintering ducks that feed in the ricefields at night and then roost by day in other wetlands (Farmer et al., 2017; Marty et al., 2020). Other granivorous birds such as corvids and game birds are likely to be key vectors of NFF weeds via endozoochory in other ecosystems (Green et al., 2019; Orłowski et al., 2016), and are also worthy of future research and spatial modelling.

4.2 | Influence of different retention time curves, and individual variation in movement

Individual variation in behaviour and gut functioning can have important consequences for seed dispersal (Zwolak, 2018). The shape of the dispersal kernel varied between individual gulls present in the same winter, owing to variation in their trajectories (Figure S4). Nevertheless, the shape of the overall dispersal kernel and the average dispersal distances were highly robust to the removal of the individuals showing the longest dispersal events (Table S3). Therefore, seed shadows generated from our models did not depend strongly on particular individuals with high mobility, but were the consequence of daily movements of all individuals.

Experimental studies of waterbird endozoochory have revealed strong variation in gut retention times and NFF seed survival between individual birds (Figuerola et al., 2010; Kleyheeg et al., 2015), and retention time curves are influenced by many factors including diet, age, stress and gender (Kleyheeg et al., 2018; van Leeuwen, Tollenaar, et al., 2012). We did not consider the differences between seven individual gulls used to generate our experimental retention time curve, but instead we compared it with a theoretical curve generated from Viana et al. (2016) and Yoshiwaka et al. (2019).

Our experimental retention curve showed shorter dispersal distances (median 690 m) than the theoretical retention curve (median 940 m), but both had a long tail typical of seed dispersal curves (Anderson et al., 2011; Morales & Carlo, 2006; Viana et al., 2013). As would be expected (Godínez-Alvarez et al., 2020), the higher mean retention time for the theoretical model generated longer-dispersal distances for most seeds. However, the seed shadows were generally similar for the two models, especially for dispersal outside ricefields. Within ricefields, the theoretical curve led to a stronger increase in dispersal distances, associated with an increased probability that a gull had moved to a nocturnal roost site before seed egestion occurred. Median distances for seed dispersal by *L. fuscus* are likely to be lower in ricefields than in some other habitats, since *L. fuscus* have been found to move distances of 40–80 km on a daily basis to reach feeding sites in previous studies (Martín-Vélez et al., 2019; Thaxter et al., 2015).

It is unclear whether the most accurate retention time curves are generated by experiments in captivity or by theoretical curves (Viana et al., 2013; Yoshikawa et al., 2019). Results in captivity may be influenced by the lack of flying activity. Kleyheeg et al. (2015) found that seed passage through the digestive tract of mallards

increased by up to 80% with physical activity compared with animals resting in conventional cages, but there was little effect on the shape of the retention time curve. We did not study long-distance migratory flights, hence captive experiments may reasonably reflect the field conditions in which gulls were spending the majority of the day stationary, and often roosting after completing a feeding bout.

Normally, variation in traits such as seed size and hardness influence the retention time curves of individual NFF taxa (Figuerola et al., 2010; Lovas-Kiss et al., 2020). However, in our case, all four taxa (with similarly small seeds) showed the same retention curves, so the seed dispersal kernels generated from our models were equally valid for the four different taxa. Similar seed shadows can be expected for other plants with similar seed traits dispersed by *L. fuscus* in our study area (Table S1).

4.3 | Seed dispersal within the ricefield complex

A strong majority (around 92%) of dispersed seeds were deposited within the ricefield area, in both models. This was expected given the dominance of gull-days in which birds remained within the 360 km² ricefields, which provide both foraging and roosting habitat, and are so extensive that seeds can be dispersed up to 41 km and still be deposited within ricefields (Table 1). The spatial dynamics of the rice harvest, in which different fields are harvested sequentially rather than simultaneously, provides enough resources for individual gulls to remain in the area for days or weeks at a time (Martín-Vélez et al., 2020), dispersing weeds continuously while harvesting. Given the spatial resolution of our GPS data, we could not study the microhabitats in which seeds were deposited at a fine scale within our models, and could not be certain when gulls were inside a field or on the dykes separating fields. Gulls egest particularly high densities of seeds on dykes, paths and field edges where they typically roost (Lovas-Kiss, Sánchez, et al., 2018). As reflected in the distribution of seed dispersal distances, *L. fuscus* disperse most seeds beyond the fields where ingestion occurred. Both the length and width of individual fields in our study area are typically <500 m, and hence below the median dispersal distance within ricefields (Table 1). Hence, if a new weed or a new herbicide resistant genotype appears in one field, LBBGs are capable of spreading it quickly across the entire ricefield area.

4.4 | Seed dispersal into other habitats

The remaining 8% of the seeds were dispersed outside of ricefields (median dispersal distance 18 km) with maximum distances of 131–243 km, into a range of habitats potentially suitable for weed establishment. Around 42% of these seeds were deposited into moist or wet environments most likely to be suitable for modelled weed species (permanent irrigated habitats, along the River Guadalquivir and in other waterbodies). However, some weeds dispersed by *L. fuscus* can establish in less moist habitats, especially those with Ellenberg moisture values below 6 (Table S1). This includes the alien

A. retroflexus, which is ranked third in the list of alien invasive plants in China, due to negative impacts in wetlands and on agricultural production (Bai & Shang, 2017). The dispersal of herbicide-resistant weeds (e.g. *C. difformis*, *P. monspeliensis*, *A. retroflexus*) outside of the ricefields may have important economic implications in other crop types (Farmer et al., 2017), including the irrigated cotton, sunflowers and wheat in areas surrounding the Doñana ricefields.

The stretch of the Guadalquivir River that bisects the ricefields received high densities of seeds and is tidal, so weeds deposited there by *L. fuscus* can potentially colonize habitats upstream to Seville as well as downstream towards the sea. The capacity of seeds egested by *L. fuscus* to disperse secondarily by hydrochory should be investigated. Aquatic plants such as duckweed and charophytes are also dispersed by *L. fuscus* feeding in ricefields, as are a range of aquatic invertebrates (Table S1, see also Lovas-Kiss, Sánchez, et al., 2018). For these organisms, successful dispersal may occur to wetlands as far as Fuente de Piedra lake (118 km, Figure 2), a major roosting site for *L. fuscus* (Martín-Vélez et al., 2019, 2020). *Larus fuscus* are likely to enable a stepping stone dispersal between wetlands for a range of weeds and aquatic plants (and invertebrates). Many other wetlands >150 km from Doñana ricefields (hence outside of Figure 2) are interconnected by *L. fuscus* movements across Andalusia (Martín-Vélez et al., 2020). The MDD of 243 km under the theoretical model was to a reservoir in Jaen province in eastern Andalusia (Martín-Vélez et al., 2020).

We carried out our study at a regional scale and did not include migratory flights between breeding and wintering grounds, when greater MDDs by *L. fuscus* would be expected (Viana et al., 2016). Seed dispersal distances of 293–413 km were estimated for mallards (*Anas platyrhynchos*) during migratory flights based on GPS trajectories (Kleyheeg et al., 2019). *Larus fuscus* are likely to have an important role in long-distance weed dispersal between Andalusia, Morocco and more northerly regions of Spain during their migrations (Shamoun-Baranes et al., 2017).

When departing the ricefields, gulls often visited three landfills (Figure 2), which are foraging habitats and are also used for stopovers when *L. fuscus* move from one part of Andalusia to another (Martín-Vélez et al., 2020). In these cases, we cannot rule out the possibility that the gull individuals did not feed in ricefields during the hours immediately prior to flying to landfills, and that this may have led us to overestimate numbers of seeds dispersed along these trajectories. However, even if gulls had only been feeding in ricefields the day before they flew to landfills, the maximum retention times recorded suggest they would still disperse seeds along the route connecting the landfill and ricefields. Faecal samples collected from Andalusian landfills provide further evidence that seeds are egested at these sites (V. Martín-Vélez, A.J. Green, & M.I. Sánchez, unpubl. data).

5 | CONCLUSIONS

It is vital to recognize the importance of waterbirds in endozoochory of vascular plants lacking a fleshy fruit, many of which are widely assumed to have no mechanisms for long-distance dispersal. This

includes weeds with important implications for agricultural management, for which both humans and waterbirds are likely to be key vectors, but with different roles. Our study illustrates how seed shadows generated by waterbirds can be predicted. These vectors generate spatial dispersal patterns that are very different to those expected from recognized dispersal syndromes, demanding a revision of our understanding of plant dispersal processes. We found gulls to disperse seeds over greater distances than have been reported in seed shadows by frugivores. Similar spatial studies are needed in other waterbird-weed systems, and should ideally be integrated with studies of establishment success and population genetics of weeds growing in different habitats.

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AUTHORS' CONTRIBUTIONS

V.M.-V. Formal analysis, visualization, roles/writing—original draft, conceptualization, methodology; C.H.A.v.L. conceptualization, methodology, funding acquisition; co-writing original draft—review and editing; M.I.S.: resources, writing—review and editing; F.H.: resources; J.S.-B.: resources, writing—review and editing; C.B.T.: resources, writing—review and editing; L.L.: resources, writing—review and editing; C.J.C.: resources; A.J.G.: conceptualization, funding acquisition, methodology, supervision, co-writing original draft, review and editing.










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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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