

High levels of seed dispersal by a declining wintering population of migratory geese

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Abstract

1. Ducks are known to be important seed dispersers, but the role of geese in plant dispersal is less clear. Wintering populations of migratory geese are undergoing rapid changes in distribution and habitat use in response to climate change and changes in land use, and the implications for seed dispersal have not previously been studied. At the southern end of Eurasian goose flyways, numbers are declining through short-stopping.
2. The Doñana wetlands, or 'marismas del Guadalquivir', in south-west Spain were formerly Europe's most important wintering grounds for the greylag goose *Anser anser*. There, we collected 151 faecal samples to compare seed dispersal by endozoochory in early and late winter in natural marshes and ricefields. We also tested seed germinability and simulated potential seed dispersal distances to assess the importance of this decreasing wintering population for dispersal of dry-fruited plants previously assumed to rely on abiotic seed dispersal over short distances.
3. We retrieved 1196 intact seeds belonging to 24 different taxa, including eight species not previously reported from waterfowl (Anatidae) vectors. Seeds were present in 47% of samples, with a peak of 90% in natural marshes in November, compared to only 27% in ricefields at the same time, or in the same marsh site in February. Seed abundance and richness per sample were significantly higher in early than late winter, and in natural compared to in artificial wetlands. Major differences in plant species composition between sampling sites were partly related to habitat differences and moisture requirements of individual species. Germinability in aquatic plants was higher when gut passage was followed by cold storage for 2 months prior to germination tests.
4. We simulated seed dispersal events to and from our sampling sites using GPS tracking of three geese. This suggested that seeds can be dispersed up to 25 km during daily movements, with a median of 0.2–5 km, depending on the sampling site. The most frequent dispersal syndrome assigned to the plant species

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dispersed by geese was barochory (gravity), and geese disperse plants much farther than the mechanisms predicted by their syndromes.

5. Geese likely have an important role in the dispersal and connectivity of plant populations within and beyond Mediterranean wetlands, providing an ecosystem service which is threatened by changes in migratory behaviour. Our results highlight the importance of studying seed dispersal interactions involving migratory waterbirds in the current context of species loss and distribution shifts, as many crucial interactions may be disappearing even before they are discovered.

KEYWORDS

Anser anser, endozoochory, GPS tracking, long-distance dispersal, marshlands, ricefields

1 | INTRODUCTION

Seed dispersal is a key phase in plant population demography, allowing plants to colonize new areas and escape natural enemies and competition with siblings and parents (Beckman & Sullivan, 2023). To understand and predict seed dispersal, many studies have relied on classical dispersal syndromes, based mainly on morphological traits of diaspores (Tamme et al., 2014; Vargas et al., 2023). These syndromes assume that only plants with fleshy fruits are adapted to disperse by vertebrates through endozoochory (i.e. internal dispersal of seeds by gut passage). Thus, many studies address dispersal interactions between plants and frugivorous vertebrates (e.g. González-Varo et al., 2021; Jordano et al., 2011).

However, it is now clear that classical syndromes often make poor predictions of how plants disperse in the field and ignore the widespread endozoochory of plants without fleshy fruits (Green et al., 2022). Many plant species assigned to other dispersal syndromes are dispersed by vertebrates internally, a process of 'non-classical endozoochory' (Green et al., 2019, 2022). Waterbirds have been shown to be important seed dispersers by non-classical endozoochory, dispersing both terrestrial and aquatic plants, and are especially important for long-distance dispersal (Martín-Vélez, Leeuwen et al., 2021; Navarro-Ramos et al., 2022; Soons et al., 2016; Urgyán et al., 2023). However, information on seed dispersal by waterbirds is still limited, with most studies focused on dabbling ducks (Almeida et al., 2022), and more studies are needed to identify unknown dispersal interactions since they have important implications for biodiversity maintenance (Green et al., 2023).

Changes in land use provide new opportunities for effective seed dispersal by waterbirds. Globally, 21% of natural wetlands have been lost since 1700, and an important fraction of these have been transformed into ricefields (Fluet-Chouinard et al., 2023). Waterbirds make use of ricefields and other artificial wetlands and often move between them and natural wetlands on a daily basis (Almeida et al., 2020; Pernollet et al., 2015; Sánchez-Guzmán et al., 2007). Land-use change can modify seed dispersal interactions and the chances of plant establishment in different habitats. For example, seeds of weeds and alien species have been shown to be dispersed

by ducks (Farmer et al., 2017; Urgyán et al., 2023), geese (Farmer et al., 2017; Navarro-Ramos et al., 2024), gulls and storks (Martín-Vélez, Lovas-Kiss et al., 2021) when moving between croplands and natural wetlands. By combining animal tracking data with data on seed retention time in avian guts, it is possible to estimate where ingested seeds can be deposited, and their dispersal distances (Fell et al., 2023). The integration of GPS tracking data in seed dispersal studies has grown in recent years, especially for frugivores (Ando et al., 2024; Fell et al., 2023). However, there are only a handful of studies on waterbirds that combine movement data with faecal sampling to quantify seed dispersal (Lovas-Kiss et al., 2023; Martín-Vélez, Leeuwen et al., 2021; Navarro-Ramos et al., 2024).

Geese are herbivorous and may often ingest seeds together with leaves and stems when foraging, following the 'foliage is the fruit' hypothesis (Green et al., 2022; Janzen, 1984). The greylag geese *Anser anser* is Eurasia's most abundant goose species and has great potential as a seed vector, but studies to date have focused mainly on the breeding grounds in Sweden (Hattermann et al., 2019; Navarro-Ramos et al., 2024; but see Tóth et al., 2016), with no previous studies from southern wintering grounds. Plant diversity is higher at southern latitudes, and ducks disperse more plant species by endozoochory in the Mediterranean region than in northern Europe (Brochet et al., 2009). Due to their daily movements between roosting and foraging sites, greylag geese can connect natural and artificial habitats, whether terrestrial or aquatic, and potentially disperse plant species between them (Navarro-Ramos et al., 2024).

Our present study represents the most detailed investigation of endozoochory by wintering geese. We assessed the role of greylag geese as seed dispersers in the wintering area of Doñana in south-west Spain. Greylag goose populations breeding in North-west Europe historically wintered mainly in south-western Spain, especially in Doñana (Andersson et al., 2001). However, this pattern has changed in recent decades in response to global change, with rapid increases in the number of geese wintering closer to their breeding areas in northern Europe (Månsson et al., 2022; Nilsson & Kampe-Persson, 2018), and 2023 as the year with the lowest number (9588) of geese counted in Doñana since records began in 1973 (Martínez

et al., 2023). Furthermore, geese wintering in Doñana arrive progressively later over time (Ramo et al., 2015).

The habitat suitability in this area changes during the course of a winter, leading geese to shift their distribution and habitat choice between early and late winter. We undertook sampling events covering the main feeding areas in each period, including artificial (ricefields) and natural (seasonal marsh) habitats. Our specific objectives were to (1) identify the plant species that are dispersed, together with their dispersal syndromes, habitat requirements, weed and alien status and flowering phenology (as a proxy for fruiting); (2) identify differences in abundance and richness of seeds dispersed in different habitats and at different times in the winter; (3) assess germinability of seeds in faeces, and how that depends on the delay between field collection and seed extraction in the laboratory; and (4) use GPS-tracked geese to estimate the spatial distribution of seeds dispersed, including dispersal distances and habitats into which seeds could be deposited, and whether dispersal between feeding sites is non-directional (i.e. equal dispersal from A to B, and from B to A) or directional.

Our initial hypotheses were that (1) within a foraging site, seed abundance and diversity in faeces would be higher in early than in late winter, as seeds are likely to be released from plants before midwinter, making ingestion with foliage less likely over time, and studies at higher latitudes suggest a greater abundance and diversity in geese faeces during autumn than spring migration (Lovas-Kiss et al., 2023); (2) within a sampling period, seed abundance (excluding rice) and richness would be higher in natural wetlands than in ricefields, which are likely to have a simplified plant community; (3) changes in plant species dispersed in different areas of natural wetlands will be explained by habitat features such as depth; (4) germinability of seeds would reduce as storage time between faecal sampling and seed extraction increased (Martín-Vélez, Lovas-Kiss et al., 2021); and (5) dispersal distances by endozoochory would greatly exceed those predicted by the classical dispersal syndromes assigned to the species recorded (Martín-Vélez, Leeuwen et al., 2021).

2 | METHODS

2.1 | Study species and study area

Doñana (36° 59' N, 6° 27' W) contains natural marshes ('marismas del Guadalquivir') and ponds protected in a National Park and World Heritage Site, as well as ricefields, fish farms and salt ponds, and is one of Europe's largest and most biodiverse wetland complexes (Green, Bustamante et al., 2018). Doñana has a subhumid Mediterranean climate, with most precipitation in autumn and winter, hot and dry summers, and increasingly mild winters (Green, Bustamante, et al., 2018). The numbers of geese in Doñana are highest in those winters when the natural marshes are flooded extensively, but the depth is not too high (Almaraz et al., 2012). Geese feed largely on tubers of sea club-rush *Bolboschoenus maritimus* and shore club-rush *Schoenoplectus litoralis* in the natural marsh, which

are most accessible at intermediate depths. They also feed in pastures and ricefields, especially in early winter just after rice harvest, when winter rains have not yet flooded the natural marshes (Amat et al., 1991; Martínez-Haro et al., 2013; see also van Rees et al., 2021 for seasonal availability of ricefields for waterbirds).

Our study period was particularly dry, with a total precipitation of 114.8mm between September 2021 and February 2022, compared with the historic mean of 393.6mm (1979–2021, Doñana Biological Station monitoring data). As a result, numbers of geese were relatively low, with only small areas of natural marshes that became flooded and were available for feeding (see also Fox et al., 2023). There were about 2000 geese present in November and February in our study area, although numbers peaked at around 12,000 geese in January.

2.2 | Faecal sample collection and processing

In early and late winter, we sampled the main areas where geese were concentrated at the time, based on monitoring data. Early winter samples were collected on 25 November 2021 from marshes (El Rocío, the first area to flood when rains arrive; ERN) and ricefields (Hato Blanco; HBN), where geese were feeding during the day. By late winter, ricefields were dry and had been abandoned, whereas rainfall had increased the area of natural marshes where geese were feeding. We therefore resampled El Rocío on 10 February 2022 (ERF), plus two other sites in natural marshes: El Hondón (EHF) the same day and El Cornejo (ECF) on 8 February 2022 (Figure 1). Thus, altogether we carried out five sampling events (ERN, HBN, ERF, EHF and ECF) covering four different sampling sites, resampling only at El Rocío. El Rocío is at the mouth of several entry streams and is particularly fresh compared with El Cornejo, which is brackish and situated towards the centre of marsh. El Hondón is at the southern edge of the marsh where there is influence from fresh groundwater (Paredes et al., 2021; Figure 1).

In each case, we first located monospecific geese flocks of ≥ 50 individuals and waited until they left the area. Then, we collected fresh faeces that were located out of water and separated by ≥ 2 m to minimize resampling the same individuals. Greylags egest a mean of 1.2 faeces per hour (Hahn et al., 2008). To avoid contamination from the substrate, faeces were picked up with tweezers and any part in contact with soil was removed with a knife. They were inspected with the naked eye, removing any items attached on the outside (e.g. fresh non-ingested vegetation fragments), then refrigerated in zip bags at 4°C until processing in the laboratory. Samples were processed 1–155 days after collection. This delay can influence germination patterns (Martín-Vélez, Lovas-Kiss et al., 2021).

Faecal samples were weighed, sieved (100µm mesh) and inspected under a stereomicroscope in petri dishes for intact diaspores (from here on, 'seed' although we include other diaspores such as algal oogonia). No intact rice grains were recorded. Intact seeds were measured and photographed with ZEN 2-2.0 software (Carl-Zeiss) for later identification to the lowest possible taxonomic

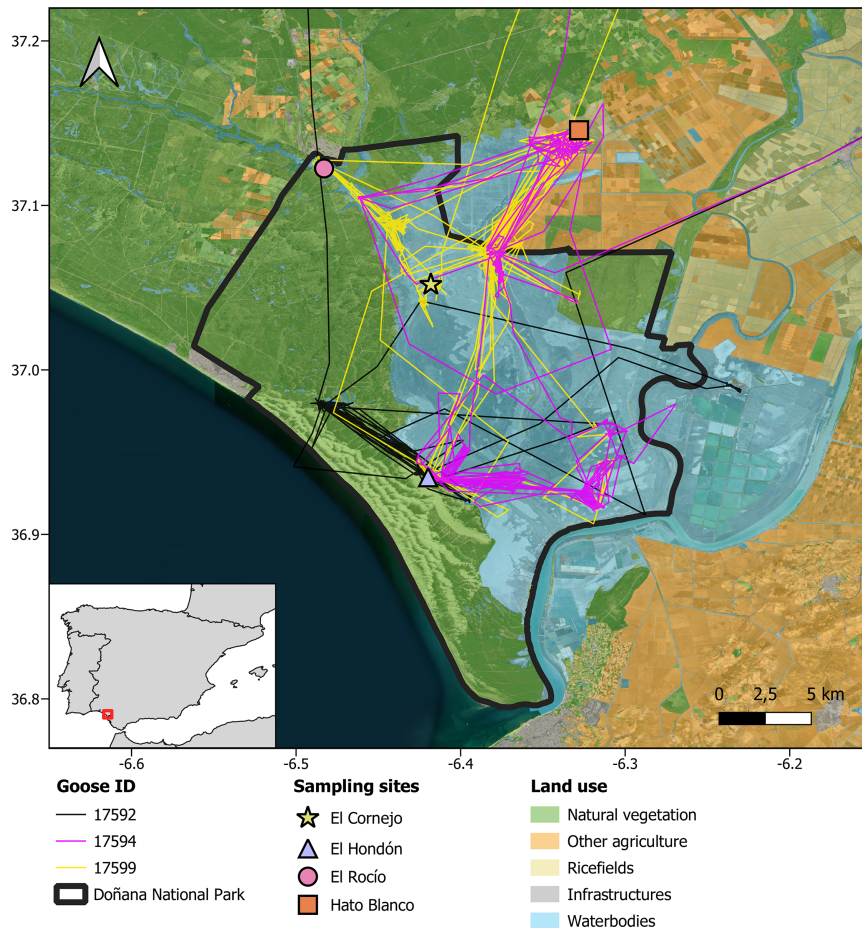


FIGURE 1 GPS data for three tagged greylag geese within the study area between 6 November 2021 and 8 February 2022. The geese arrived on 6 (17,599) or 23 November (17,592, 17,594, two parallel lines indicate how they arrived in the same flock from the north-east) and departed on 2 (17,592), 7 (17,594) or 8 (17,599) February.

level (Bojnanský & Fargašová, 2007; Cappers et al., 2012; García-Murillo et al., 2014). Seeds were then placed in multiwell plates with filter paper in a germination chamber with a 12/12h photoperiod and 18–22°C temperature. They were watered and checked for germination every 2 days for 2 months. Any seeds infected by fungi were removed to avoid contamination and scored as not germinated.

For each plant species dispersed, we extracted the Ellenberg F habitat indicator for soil moisture, seed length and dispersal syndrome from the baseflor database (Julve, 1998), and information on the flowering period in Doñana from Valdés et al. (1987). No specific data on fruiting periods were available. We also identified any alien species or agricultural weeds (Afonin et al., 2008). We consulted recent literature (Almeida et al., 2022; Lovas-Kiss et al., 2023; Navarro-Ramos et al., 2024; Tóth et al., 2023) to identify plant taxa previously shown to be dispersed by waterfowl endozoochory.

We collected one additional sample at El Cornejo that contained particularly high seed numbers. This sample was excluded from seed abundance and richness analyses, because we collected it precisely because the visible seeds caught our attention (Figure S1). For this sample, we were able to study the effect of storage time on germinability and time to germination. Thus, one subsample was placed for germination the same day it was collected, and another subsample was placed after 64 days storage in the refrigerator at 4°C.

2.3 | Seed data analyses

Differences in seed abundance and richness per sample between our five sampling events (two sites in early and three in late winter) were evaluated by applying two generalized linear models (GLMs) with sampling event (factor of five levels) and sample mass (log-transformed) as explanatory variables. When seed abundance including zeros was the dependent variable, a negative binomial error distribution was used with a log-link function, with the *glm.nb()* function from the *MASS* package (Venables & Ripley, 2002). When seed richness per sample was the dependent variable, samples without seeds were excluded, and a Poisson error distribution was used with the *glm()* function. Quantile–quantile plots with fitted values were examined to confirm homocedasticity and absence of overdispersion. The fitness of the models was assessed by calculating the Nagelkerke pseudo r-squared (Nagelkerke, 1991) with the *nagelkerke()* function from the *rcompanion* package (Mangiafico, 2020). To identify differences in seed abundance and richness between sampling events, pairwise comparisons were performed using the *estimate_contrasts()* function from the *modelbased* package (Makowski et al., 2020), applying Bonferroni correction for multiple testing.

For each sampling event, rarefaction curves were calculated for changes in overall taxonomic richness according to sample size, using the *specaccum()* function of the package *vegan* (Oksanen et al., 2022). To discern differences in plant species composition

between sampling events, non-metric multidimensional scaling (NMDS) was performed with the function *metaMDS()* from the *vegan* package (Oksanen et al., 2022), employing a Bray-Curtis distance matrix.

The effect of the delay between field collection and sample processing on germinability was evaluated with a two-proportion Z test using the *prop.test()* function. To test the effect of storage on germination time, Kaplan-Meier survival curves were fitted using the *survfit()* function, and a log-rank test was used to assess if they were significantly different with the *survdiff()* function from the *survival* package (Therneau, 2023). For germination time analyses, only seeds that germinated within 2 months were used.

All data management and statistical analyses were performed in R software, version 4.2.1. (R Core Team, 2022).

2.4 | Geese tracking data and movement analysis

We used GPS data from three greylag geese caught in Denmark in June 2021 and fitted with Ornitela OT-N35-3G 35g GPS/GSM tracking collars set to record positions every 10 min (details in Fox et al., 2023). These birds spent the winter of 2021–2022 in Doñana (Figure 1).

We defined spatial polygons covering the area of the four faecal sampling sites using satellite imagery, land-use information (Junta de Andalucía, 2023) and GPS-tracking data, and selected the GPS fixes located within them up to 1 month before and after each faecal sampling date. We simulated dispersal events that start with the ingestion of seeds and end with their egestion in faeces. Seeds can both be moved to faecal sampling sites by geese arriving and moved away from them when geese leave. Hence, for each fix within these sampling sites polygons, we selected all the fixes for the same individual goose made from 30 min to 12 h beforehand, and afterwards. We chose 30 min to 12 h intervals because 90.6% of seeds recovered from captive greylag goose faeces were egested within 12 h (García-Álvarez et al., 2015). For the locations of each of these selected fixes, we extracted information on land use from a pre-existing map (Junta de Andalucía, 2023) and calculated the distance to the fix of origin (i.e. within our faecal sampling polygons) using the *pointDistance* function in the *raster* R package (Hijmans, 2023). Locations selected in the 12 h interval before fixes at sampling sites represent places where geese may have ingested seeds deposited in the sampling polygons. To exclude GPS tracking data for locations recorded while birds were in flight, based on a speed histogram of GPS data, recorded locations were filtered to keep only those that show movement speeds of <5 km/h. Night-time locations were not excluded as geese can forage throughout the 24-h period (Kahlert et al., 1996). Locations selected in the 12 h interval after being at sampling sites represent places to which geese may have dispersed seeds ingested at those sites. Geometric means of simulated seed dispersal distances were calculated, adding 1 m to the distance value of each simulated endozoochory event to eliminate zeros.

Data management and analyses were performed in QGIS, version 3.22.12 (QGIS.org, 2024), and R software, version 4.2.1. (R Core Team, 2022).

3 | RESULTS

3.1 | Seed data

We analysed 151 faecal samples with a mean weight of 7.76 g (± 4.75 SD; range 1.38–28.19 g). We excluded one sample collected because of its extreme seed density. For the remaining samples, a total of 1196 intact seeds were retrieved, with 47% of samples containing at least one intact seed. The average number of seeds per sample was 7.97 (± 23.30 SD; range 0–153). For samples with ≥ 1 seed, the mean number of seeds was 17 ± 31.8 SD (median = 3).

We found 24 different plant taxa from 15 different families (Table 1). We identified 18 taxa at the species level, three others at genus and another three at the family level. Most taxa were vascular plants, but charophytes (*Tolypella* spp.) were also recorded. We found eight plant species not previously reported as dispersed by waterfowl endozoochory (Table 1). Previously assigned dispersal syndromes were barochory (i.e. gravity, six species), anemochory (wind, two species), epizoochory (external attachment, five) and hydrochory (water, three). According to Ellenberg moisture values (Table 1), one species occupies dry soils ($F \leq 4$), 10 are typical of moist or wet soils ($5 \leq F \leq 8$) and five are aquatic plants ($F \geq 9$). None of the species were introduced to Spain. Three were agricultural weeds (Table 1). The flowering period varied widely, but only started before March for *Ranunculus* spp. (Table 1). Flowering ended over a 9-month period ranging from April (*Eleocharis palustris*) to December (*Trifolium repens*). Seed length ranged from 0.37 to 3.73 mm (Table 1). Germinability was confirmed for 67 seeds from five different plant taxa, plus a sixth taxon from the sample used to study the effect of storage time (Table 1).

Among sampling events, ECF showed the highest mean Ellenberg moisture value for all seeds, while it was similar among four other events (Table S1). The species with the earliest flowering periods were present in ECF and EHF, starting in January, while ERF presented the one finishing later, in December. All species found in November samples have flowering periods between March and October (Table S1).

There were significant differences between sampling events both for seed abundance and seed richness per sample, and heavier samples showed significantly higher numbers of seeds and taxa (Table 2). ERN significantly exceeded all other sampling events in seed abundance and richness per sample (Table 2 and Table S2) and had higher seed prevalence and total number of different taxa than other events (Table S1). The dominant species in ERN was *Sporobolus aculeatus*, which was absent from other events. Dominant taxa differed between ERN and HBN samples collected the same day, the latter being dominated by *Heliotropium supinum* and *Juncus bufonius* (Figure S2).

TABLE 1 Details of intact seeds recovered from greylag geese faeces. Species not previously reported as dispersed by waterfowl endozoochory are marked in bold.

Family	Species	Dispersal syndrome	Ellenberg F	Length (mm)	Flowering period	G	N	MS	NST	Sampling events
Alismataceae	<i>Damasonium polyspermum</i>	Barochory	8	1.53	April–June	No	3	1	3	ECF
Apiaceae	<i>Eryngium</i> sp.	–	–	3.73	–	No	1	1	1	ERN
Asteraceae	Unidentified Asteraceae	–	–	0.77	–	No	2	1	2	EHF
Caryophyllaceae	Unidentified Caryophyllaceae	–	–	0.55	–	No	1	1	1	ERN
Characeae	<i>Tolypella glomerata</i>	–	–	0.37	–	No	3	2	2	ERN
Characeae	<i>Tolypella</i> sp.	–	–	0.3	–	No	1	1	1	EHF
Cyperaceae	<i>Bolboschoenus maritimus</i> ^a	Anemochory	9	2.74	April–June	No ^b	13	5	7	ERN, ECF, EHF
Cyperaceae	<i>Carex</i> sp.	–	–	1.4	–	No	1	1	1	ERN
Cyperaceae	Unidentified Cyperaceae	–	–	1.32	–	No	1	1	1	ERN
Cyperaceae	<i>Cyperus fuscus</i>	Barochory	8	0.96	July–October	No	1	1	1	EHF
Cyperaceae	<i>Eleocharis palustris</i>	Epizoochory	8	1.81	March–April	Yes	7	3	5	ERN, ECF, EHF
Cyperaceae	<i>Pycreus flavescens</i>	Barochory	7	0.98	August–November	No	1	1	1	EHF
Cyperaceae	<i>Schoenoplectus litoralis</i>	Anemochory	9	1.73	May–June	No	2	1	2	ECF, HBN
Elatinaceae	<i>Elatine campylosperma</i>	Barochory	8	0.46	April–June	No	15	5	7	ERN, ECF, EHF
Fabaceae	<i>Melilotus albus</i>	Epizoochory	4	1.86	May	Yes	1	1	1	ERN
Fabaceae	<i>Trifolium repens</i>	Epizoochory	7	1.3	March–December	No	1	1	1	ERN
Heliotropiaceae	<i>Heliotropium supinum</i>	Barochory	7	2.69	May–October	Yes	260	29	36	ERN, ERF, HBN
Juncaceae	<i>Juncus bufonius</i> agg. ^a	Epizoochory	7	0.46	March–August	Yes	95	53	19	ERF, EHF, HBN
Lamiaceae	<i>Mentha pulegium</i>	Epizoochory	8	0.88	May–November	No	2	2	1	ERN
Poaceae	<i>Sporobolus aculeatus</i>	Barochory	8	1.57	June–October	Yes	776	129	22	ERN
Polygonaceae	<i>Rumex dentatus</i> ^a	Hydrochory	–	1.72	April–October	No	3	1	3	ERN
Ranunculaceae	<i>Ranunculus baudotii</i>	Hydrochory	11	1.09	January–May	No	1	1	1	EHF
Ranunculaceae	<i>Ranunculus trichophyllus</i>	Hydrochory	11	1.03	January–May	No	4	2	3	ECF, EHF
Typhaceae	<i>Typha domingensis</i>	Anemochory	9	0.76	July–November	No	1	1	1	EHF
Total							1196			

Abbreviations: G, whether or not germinability was confirmed in this study; MS, the maximum number of seeds in one sample; N, the total number of intact seeds retrieved per taxon; NST, number of samples containing seeds of that taxon.

^aSpecies considered agricultural weeds.

^bSeeds were germinated in an additional sample (Figure S2).

The lack of overlap in confidence intervals indicates that many of the differences in total richness between sampling events were significant (Figure S3).

3.2 | Sample storage and germinability

The additional sample (Figure S1) contained a total of 521 seeds. The subsample processed first (SBP 1) weighed 4.46g and the second (SBP 2) 14.90g. Seeds of three different plant species were recorded: *B. maritimus* ($N_{SBP1}=64$; $N_{SBP2}=224$), *E. palustris* ($N_{SBP1}=57$, $N_{SBP2}=174$) and *S. litoralis* ($N_{S2}=2$). Storage for 64 days significantly increased germinability of *E. palustris* seeds from 58% to 75% ($p=0.02$) and of *B. maritimus* from 11% to 27% ($p=0.01$; Figure S4). Germination time was longer after storage for *E. palustris* seeds, but this difference was not significant ($p=0.26$; Figure S5). Seeds of *B. maritimus* took significantly longer to germinate after storage ($p<0.0001$, Figure S5).

3.3 | Movement analysis

Geese tracking data showed how geese flocks were moving to and from the faecal sampling sites, and flying between them (Figure 1). We filtered 5036 geese GPS fixes within the five sampling event

polygons (Table S3). For each polygon, we had fixes of one or two geese (Table S3). Locations of simulated seed dispersal events were predictably clustered within the polygons, but also in adjacent areas of ricefields and other areas of the marshlands (Figure 3 and Figure S6). Most dispersal events starting or ending at Hato Blanco included ricefields or other agricultural fields, whereas the dispersal events to or from marshland sites encompassed mostly natural marshlands and other wetlands (Figure S7). In part, dispersal was directional. Seeds were dispersed from El Rocío, El Cornejo and El Hondón to Hato Blanco (i.e. from natural marshes to ricefields), but not in opposing directions (Figure 3 and Figures S6 and S7, these dispersal events involved two individuals).

Geometric mean dispersal distances were 0.25 km for dispersal events starting at faecal sampling sites and 0.24 km for dispersal events ending at the sampling sites, with differences in means and maxima between sampling sites, and maxima exceeding 14 km at all four sampling sites (Table 3).

4 | DISCUSSION

Greylag geese wintering in south-west Spain were dispersing at least 24 angiosperm or charophyte species by endozoochory. None of the species recorded has a fleshy fruit, and they represent a wide variety of soil moisture preferences, seed sizes, flowering periods

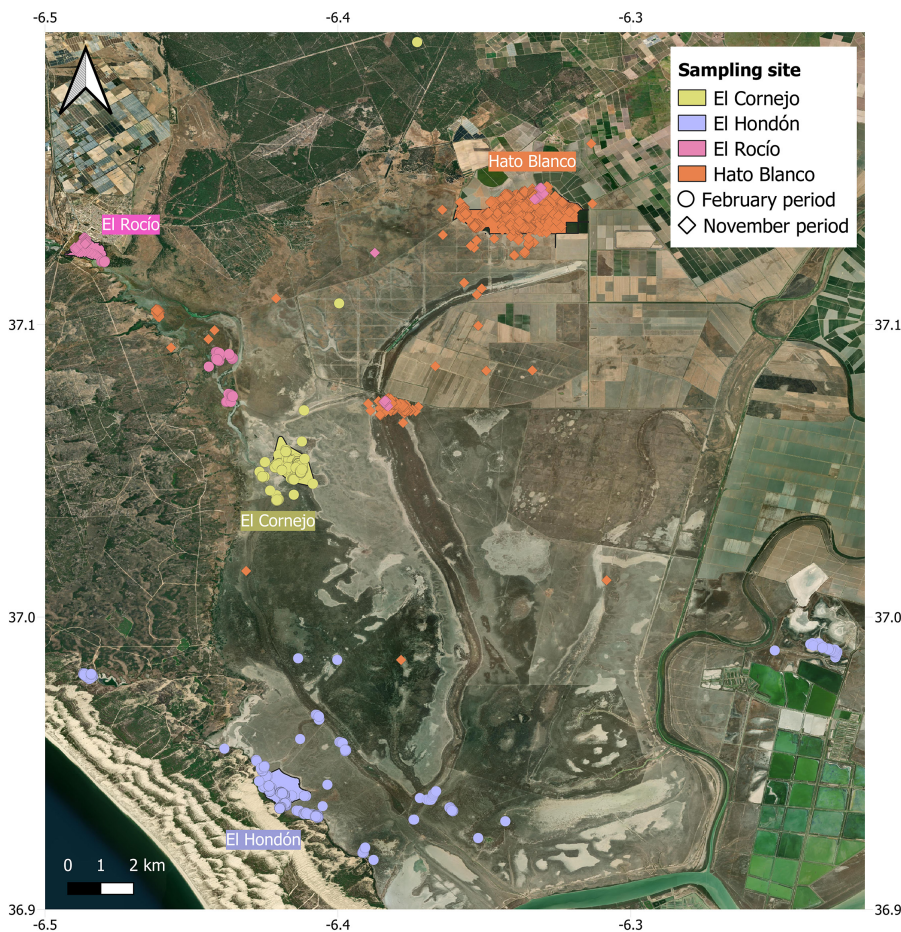


FIGURE 3 Simulated seed deposition locations for endozoochory events starting at the four faecal sampling sites. Nineteen per cent of the locations are situated outside the polygon of origin. Note how seeds can be dispersed from El Rocío to Hato Blanco, but not the other way around.

TABLE 3 Distances of simulated endozoochory events starting (a) and ending (b) at the sampling sites. Geometric means, quantiles and maximum distances are shown for each sampling event. In order to calculate geometric means, 1 m was added to the distance value of each simulated endozoochory event, to eliminate zeros.

Sampling event	Dispersal distance (km)				
	Geometric mean (95% CI)	25%	50%	75%	Max
(a)					
ECF	0.13 (0.13–0.14)	0.06	0.19	0.33	17.03
EHF	0.29 (0.28–0.29)	0.05	0.46	1.17	17.16
ERN	0.76 (0.73–0.79)	0.20	0.66	10.93	14.27
ERF	4.47 (4.25–4.70)	5.03	5.10	6.41	6.62
HBN	0.29 (0.29–0.29)	0.05	0.22	1.20	16.99
(b)					
ECF	0.14 (0.14–0.14)	0.06	0.20	0.34	1.85
EHF	0.28 (0.27–0.29)	0.05	0.47	1.19	7.84
ERN	0.46 (0.45–0.47)	0.20	0.62	2.36	2.88
ERF	4.06 (3.86–4.27)	4.97	5.01	5.03	5.11
HBN	0.28 (0.27–0.28)	0.05	0.21	1.03	25.18

and dispersal syndromes. Both the number of seeds and species dispersed varied among different sites and between the beginning and the end of the wintering season. GPS data from three tagged geese allowed us to document how geese connected the different sites and were able to disperse seeds over greater distances than those recently predicted (Lososová et al., 2023) based on their dispersal syndromes.

4.1 | Unusually high rates of non-classical endozoochory

None of the species we found to be dispersed by goose endozoochory have been assigned to the endozoochory dispersal syndrome. This confirms the vital importance of differentiating between the currently ascribed syndromes and the actual mechanisms of dispersal used by plants (Green et al., 2022). Syndromes, assigned via visual inspection of plant morphology, are only hypotheses about potential adaptations to a specific dispersal mechanism and should not be equated with mechanisms (Vargas et al., 2023). Unfortunately, potential adaptations for endozoochory in dry-fruited plants are not contemplated (Costea et al., 2019; Green et al., 2023). To our knowledge, this is the first study of seed dispersal by geese in southern Europe or a Mediterranean biome, and the most detailed study of endozoochory by wintering greylag geese. We found relatively high prevalence (47%) and abundance of seeds compared with previous studies of goose endozoochory, reaching levels that are typical of dabbling duck studies (e.g. Urgyán et al., 2023). Considering the numbers of geese wintering in Doñana (see methods), the numbers of viable seeds dispersed daily during the winter period were likely to exceed 100,000. A summer study of greylag geese in Sweden recorded seeds in only 10% of faecal samples (Navarro-Ramos et al., 2024). Regarding other geese species, Lovas-Kiss et al. (2023) found that 12% of pink-footed goose (*Anser brachyrhynchus*) samples in the UK contained ≥ 1 intact seed. For Canada geese (*Branta canadensis*), the seed prevalence was only 8.4% in samples from

England (Tóth et al., 2023). On the other hand, where geese feed heavily on fleshy-fruits in their breeding ranges, higher prevalences have been recorded: 78% for Canada geese in Greenland (Green, Lovas-Kiss et al., 2018) and 72% for pink-feet in Iceland (Lovas-Kiss et al., 2023). However, even these figures were exceeded by the 90% of samples we found with seeds in ERN. Our high rates of endozoochory are likely to be connected with the importance of natural wetlands as a feeding habitat, compared to the dominance of agricultural fields for foraging in many other wintering and breeding areas for this flyway population of greylag geese.

Many plant species we recorded (44%) had not been previously reported to be dispersed by waterfowl. Our results improve the understanding of what plants are dispersed by non-classical endozoochory and suggest there still remain many such dispersal interactions to be described, despite recent advances in the study of waterbird zoochory (Almeida et al., 2022; Green et al., 2023). Indeed, rarefaction analyses (Figure S3) predicted that we would have found more species by increasing sample sizes, a pattern repeated in other studies of waterbird endozoochory (e.g. Martín-Vélez, Lovas-Kiss et al., 2021; Navarro-Ramos et al., 2022, 2024).

4.2 | Seasonal variation in endozoochory

We expected to find more seeds being dispersed in November than February according to the timing of fruit production, and although flowering periods of the species dispersed varied greatly, most started flowering after February but finished before November, so therefore seed availability was highest in November. We were not able to sample geese in Hato Blanco, El Cornejo or El Hondón in both months, because geese changed their distributions in response to dynamic flooding conditions. For the site sampled in both months, El Rocío, seeds were much more abundant in November faeces, as expected. However, the number of different taxa found in February samples (14) was also high, and six of them were shared with samples from November (Table 1).

These results suggest variation in ways seeds are ingested, and that geese can disperse seeds outside the fruiting period of the plants by feeding on seeds that are floating when wetlands are flooded, or directly from the seed bank, as has been demonstrated for other waterbird species (Martín-Vélez, Lovas-Kiss et al., 2021; Urgyán et al., 2023). Geese in marsh areas such as El Cornejo and El Hondón usually feed on *B. maritimus* and *S. litoralis* tubers (Amat et al., 1991), during which they may accidentally ingest seeds from the mud or the water. Our exceptional sample from ECF (Figure S1) is more likely to be from a goose that was intentionally feeding on seeds, perhaps concentrated by water movement when that area was first flooded by heavy rains. Similarly, geese intentionally feed on loose rice grains in ricefields, as confirmed by rice fragments in faeces.

Geese also intentionally eat dry fruits from the mother plant, or incidentally when feeding on foliage (Almeida et al., 2022; Middleton & Van der Valk, 1987). An obvious example is *S. aculeatus*, the most abundant seed dispersed in November during its fruit ripening period, with many seeds recovered from faeces still inside their floral envelopes (Figure S8).

4.3 | Differences in seed dispersal between natural and artificial wetlands

We found evidence that seeds are dispersed between natural and artificial wetlands, but that most seeds are dispersed locally (i.e. within each of our four sampling sites). We found support for our initial hypothesis that seed abundance and richness are higher in natural wetlands. In November, faecal samples from natural marshes (i.e. El Rocío) had significantly more seeds and plant species than samples from artificial wetlands (ricefields). Furthermore, while all three natural marsh sites had at least one unique plant species recorded only there, all three plant species found in ricefields were also recorded in natural marshes (Figure 2). Of these, *J. bufonius* is an abundant ricefield weed and was the dominant seed taxon in the egesta of storks and gulls feeding in the Doñana ricefields (Martín-Vélez, Lovas-Kiss et al., 2021). *Heliotropium supinum* and *S. litoralis* are not considered ricefield weeds and were not recorded in egesta of gulls or storks from the same area. It is likely that seeds of these two species recorded in geese faeces at Hato Blanco were ingested in the natural marshes. Compared to our results for geese, Martín-Vélez, Lovas-Kiss et al. (2021) found that more seeds and plant species were dispersed by storks and gulls within Doñana ricefields, including a high proportion of weeds (38%) and alien taxa (18%). This is likely connected to the importance of the alien crayfish *Procambarus clarkii* in their diet and to the greater use of natural marshes by geese (Martín-Vélez, Lovas-Kiss et al., 2021; Rendón et al., 2008). Similarly, although Doñana holds large numbers of wintering ducks, these have different habitat use than geese (Rendón et al., 2008) and disperse an overlapping, but distinct set of plants (Almeida et al., 2022; Figuerola et al., 2003).

Even within the natural marshes, we found important differences between the three sampling sites in the relative abundance

of plant species dispersed, which are compatible with the habitat differences. The higher moisture (Ellenberg F) values of seeds dispersed in El Cornejo reflect its position in the centre of the marsh site, and its domination by emergent plants, with fewer terrestrial plants than El Rocío and El Hondón situated on the marsh periphery (Figures 1 and 3).

4.4 | Germinability of seeds after gut passage

We confirmed seed germination after gut passage for six different species. However, the number of species whose seeds remain viable after gut passage is likely to be greater. The total number of seeds found in the faeces was ≤ 3 for most plant taxa, limiting the number of seeds available to test germinability after gut passage. We germinated seeds for all species for which we recovered >4 seeds, except for *E. campyloperma* (Costea et al., 2019 germinated *Elatine* spp. seeds after duck gut passage). We did not conduct any additional tests to confirm the viability of dormant seeds that did not germinate, but Navarro-Ramos et al. (2024) confirmed the viability of ungerminated seeds using tetrazolium. We recorded particularly high rates of germinability for *E. palustris* and *B. maritimus*, two of the plant species most often recorded in previous studies of waterfowl endozoochory (Almeida et al., 2022). We also found their germinability increased after cold storage of faecal samples, in contrast to results for *J. bufonius* dispersed by gulls and storks (Martín-Vélez, Lovas-Kiss et al., 2021). Similarly, Espinar et al. (2023) found that, after gut passage, cold storage in water further increased germinability of *B. maritimus* and *S. litoralis*, but observed the opposite effect for *Juncus subulatus*. Hence, both gut passage and cold storage can break dormancy for sedges (Cyperaceae) with cumulative effects, and this may favour the establishment of seeds dispersed by endozoochory by allowing them to incorporate into seed banks until conditions for growth are more suitable (Espinar et al., 2023).

4.5 | Directions and distances for seed dispersal by geese

Movement data showed how greylag geese were connecting the few restricted areas that were flooded during winter 2021–2022 in Doñana (Figure 1), dispersing seeds between them. For a seed dispersal event to be effective, the seed must be deposited in a suitable site (van Leeuwen et al., 2022). According to land-use categories and simulated dispersal events, most seeds are ingested and deposited in similar habitat types (Figure S7), illustrating how waterbirds can provide directed, non-random dispersal towards favourable sites (Kleyheeg et al., 2017).

We also found evidence of directional dispersal between our four sampling sites, in which geese were more likely to disperse seeds from natural marsh sites to ricefields than the other way around. This can be explained by factors other than food availability, such as, for instance, when geese habitually go to drink water from

natural habitats at specific times of the day or when they are displaced from feeding habitats by human or predator activity (Nilsson & Persson, 1992). Hence, geese can develop routines in which they fly to a particular feeding site from one place but return to a different place after feeding.

Most locations of simulated endozoochory events were within, or close to, the sampling polygons, with half covering distances of <0.6 km. However, there were many events exceeding 5 km, including dispersal to other polygons, and relatively long maximum dispersal distances of up to 25 km (Table 3). These dispersal distances greatly exceed the maxima predicted for these plant species in different studies relying on documented dispersal syndromes and morphological traits, which usually do not reach more than a few tens of metres (e.g. Lososová et al., 2023; Tamme et al., 2014). For example, maximum dispersal distances estimated for *J. bufonius* in the literature were one (Lososová et al., 2023) or 100 m (Tamme et al., 2014). However, it was one of the most prevalent species in our samples, together with *H. supinum* and *S. aculeatus*, whose dispersal distances were also estimated by Lososová et al. (2023) at 1 m.

Departure of geese at the time of our sampling in February (Figure 1) indicates that geese are also likely to disperse seeds northwards over much longer distances during spring migration to the breeding areas (Nilsson & Kampe-Persson, 2018). Greylag geese can retain seeds in their guts for up to at least 96 h (García-Álvarez et al., 2015) and we recorded instantaneous tag speeds up to 140 km/h during migration. For those 14 taxa we recorded in February, goose endozoochory is likely to enable plants to adjust to climate change through gene flow and shifting distributions, as reported for pink-footed geese (Lovas-Kiss et al., 2023). Moreover, three of these species are currently only present in Southern Europe (*Damasonium polyspermum*, *E. campylosperma* & *H. supinum*). To better understand the spatial patterns of seed dispersal, both local and long-distance dispersal, future studies with more tagged individuals at more localities, would be of great interest.

5 | CONCLUSION

Greylag geese are major vectors of seed dispersal for many plant taxa on southern wintering grounds, and we recorded some of the highest rates of seed movement for any goose study. Our study provides further evidence that waterfowl endozoochory is a widespread mechanism of seed dispersal for many plant species lacking fleshy fruits and that geese can be as important vectors as ducks (Almeida et al., 2022). Especially for species with particularly high dispersal rates (e.g. *S. aculeatus*, *J. bufonius*, *H. supinum*), geese may be important for maintaining connectivity between plant populations in patchy habitats. However, the proportion of the annual cycle spent by geese wintering in Doñana has been gradually reducing for decades (Ramo et al., 2015), and numbers have recently declined from 70,000 in 2016 to 10,000 in 2023 (Martínez et al., 2023). This translates to a sevenfold reduction in seed dispersal activity by this wintering goose population, which may have negative impacts on

plant populations and their capacity to respond to climatic change. Ecological interactions can disappear even before one of the species becomes locally extinct if they reach densities too low to continue interacting successfully (Jordano, 2016). This could potentially happen due to reductions in the surface area or hydroperiod of natural marshes through water extraction and climate change (Green et al., 2024). Short-stopping is being increasingly observed in goose populations undergoing long-distance migrations, and greylag geese have also declined in their former wintering grounds in North Africa (Podhrázký et al., 2017). Expected reductions in wintering geese numbers at southern latitudes will impact the seed dispersal service they provide, with important implications for plant population dynamics.

AUTHOR CONTRIBUTIONS

Conceptualization: AJG, VM-V, MJN-R. Developing methods: AJG, VM-V, MJN-R, IJ-M, AM. Data analysis: IJ-M, AM. Preparation of figures and tables: IJ-M, AM. Conducting the research: IJ-M, AM, VM-V, MJN-R, ÁL-K. Data interpretation: IJ-M, AM, AJG. Writing: all authors.

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CONFLICT OF INTEREST STATEMENT

Andy J. Green is an Editor for Freshwater Biology but has been excluded from the assignment of the handling editor, the peer review process, and all decision-making for their manuscript. Freshwater Biology encourages its Editors to publish in the journal, and their access to Scholar One is limited to separate them completely from the decision-making process for their manuscripts.

DATA AVAILABILITY STATEMENT

Data available at: <https://github.com/iciarjimm/DonanaGeeseFWB.git>.

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