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Research

Shorebirds as important vectors for plant dispersal in Europe

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Shorebirds (Charadriiformes) undergo rapid migrations with potential for long-distance dispersal (LDD) of plants. We studied the frequency of endozoochory by shorebirds in different parts of Europe covering a broad latitudinal range and different seasons. We assessed whether plants dispersed conformed to morphological dispersal syndromes. A total of 409 excreta samples (271 faeces and 138 pellets) were collected from redshank *Tringa totanus*, black-winged stilt *Himantopus himantopus*, pied avocet *Recurvirostra avosetta*, northern lapwing *Vanellus vanellus*, Eurasian curlew *Numenius arquata* and black-tailed godwit *Limosa limosa* in south-west Spain, north-west England, southern Ireland and Iceland in 2005 and 2016, and intact seeds were extracted and identified. Godwits were sampled just before or after migratory movements between England and Iceland. The germinability of seeds was tested. Intact diaspores were recovered from all bird species and study areas, and were present in 13% of samples overall. Thirteen plant families were represented, including Charophyceae and 26 angiosperm taxa. Only four species had an 'endozoochory syndrome'. Four alien species were recorded. Ellenberg values classified three species as aquatic and 20 as terrestrial. Overall, 89% of seeds were from terrestrial plants, and 11% from aquatic plants. Average seed length was higher in redshank pellets than in their faeces. Six species were germinated, none of which had an endozoochory syndrome. Seeds were recorded during spring and autumn migration. Plant species recorded have broad latitudinal ranges consistent with LDD via shorebirds. Crucially, morphological syndromes do not adequately predict LDD potential, and more empirical work is required to identify which plants are dispersed by shorebirds. Incorporating endozoochory by shorebirds and other migratory waterbirds into plant distribution models would allow us to better understand the natural processes that facilitated colonization of oceanic islands, or to improve predictions of how plants will respond to climate change, or how alien species spread.

Keywords: alien species, plant dispersal syndromes, long-distance dispersal

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The wide distribution of fresh-water plants, and of the lower animals, whether retaining the same identical form, or in some degree modified, apparently depends in main part on the wide dispersal of their seeds and eggs by animals, more especially by fresh-water birds, which have great powers of flight, and naturally travel from one piece of water to another.

Charles Darwin (1872)

Introduction

In plants, dispersal is an important determinant of distribution (Ridley 1930), therefore correctly characterising dispersal mechanisms can be crucial in understanding past and future changes in distribution related to ecological and climate changes (Wilkinson 1997, Corlett and Westcott 2013, Tamme et al. 2014). Studies examining the dispersal of plants by birds via endozoochory (i.e. dispersal of ingested diaspores that survive gut passage) have mainly focused on frugivorous species (Forget et al. 2011, Wenny et al. 2016). However, omnivorous migratory waterbirds can also act as important vectors for a wide range of plant species (Figuerola et al. 2003, Brochet et al. 2009, van Leeuwen et al. 2012, Green et al. 2016, Lovas-Kiss et al. 2018a, b). While many waterbirds undergo long-distance migrations, shorebirds (waders, Charadriiformes) can travel extreme distances (even > 5000 km), in some cases without stopping (Alves et al. 2016, Conklin et al. 2017). However, there has been relatively little modern interest in their role as vectors of plant dispersal, even though seeds are frequently ingested by most shorebird species (Green et al. 2002). Some authors have suggested that shorebirds also carry seeds within their plumage or in mud adhering to their feet (i.e. epizoochory; Carlquist 1967, Schenk and Saunders 2017), and field data supports this for microscopic diaspores (Lewis et al. 2014, see also Coughlan et al. 2017 for a review of epizoochory).

Half a century ago, ex situ experiments in captivity showed that angiosperm and algal diaspores can survive passage through the shorebird digestive tract (de Vlaming and Proctor 1968, Proctor 1966, 1968). Viable seeds were retained for up to 100–340 h in the digestive system of killdeer *Charadrius vociferus* and least sandpiper *Calidris minutilla*. The most extreme retention times were for seeds recovered from regurgitated pellets, instead of those egested in faeces (Proctor 1968). However, only a few in situ field studies have confirmed that shorebirds disperse plant seeds and other diaspores by endozoochory. While Green et al. (2013) found intact seeds of eight taxa in killdeer faeces and Sánchez et al. (2006) found viable seeds of three plant species in excreta from three shorebird species. Ridley (1930) cited evidence that shorebirds disperse the fleshy-fruited *Vaccinium*, *Empetrum* and *Canthium*. In addition, shorebirds have been shown to be important vectors for aquatic invertebrates (Green and Sánchez 2006, Sánchez et al. 2012).

On wintering and staging grounds, shorebirds regularly make daily movements of tens of km between feeding and roosting sites (Dias et al. 2006, Taft et al. 2008). During migration, owing to their rapid long-distance flights (Alves et al. 2016, Conklin et al. 2017) and their long gut retention times, shorebirds can likely transport diaspores over hundreds or even thousands of kilometres (Proctor 1968, Viana et al. 2013). This makes them particularly interesting as potential vectors for the long-distance dispersal (LDD) of propagules at transcontinental and intercontinental scales. Accordingly, shorebirds have been considered as likely vectors for historic LDD events concerning fleshy-fruited plants, particularly those that have led to their bipolar distribution (Popp et al. 2011) or colonization of oceanic islands (Carlquist 1967). Importantly, it is often assumed by researchers that endozoochory by birds is only important for plants assigned to an 'endozoochory syndrome' on the basis of having a fleshy-fruit (Tamme et al. 2014, Schenk and Saunders 2017, Correia et al. 2018). On the other hand, Darwin (1872) considered waterbirds as likely vectors for aquatic plants but not terrestrial ones (see above quote), and recent modelling has focused on their value as vectors for aquatic but not terrestrial species (Viana et al. 2013, Viana 2017). Exactly which species are dispersed, and in what quantity cannot be identified on purely theoretical grounds and requires empirical data (if only to test theoretical assumptions). Hence, new studies are required to assess the importance of shorebirds as vectors for diaspores of different plant groups.

In this empirical study, we assess whether endozoochory by shorebirds is a regular and widespread mechanism of plant dispersal in Europe, by sampling six different bird species, in contrasting habitats at varying latitudes. Our main aims were to consider: 1) is endozoochory by shorebirds a frequent process? 2) Whether this is only important for fleshy-fruited plants, or also for plants assigned to other dispersal syndromes; and 3), whether this is only important for aquatic plants, or also for plants from different habitats. We also consider whether the distributions of the dispersed plant species are consistent with LDD events that shorebirds are likely to provide, and whether current literature provides evidence that they are dispersed by other animal vectors. We also consider differences in seed size and quantity between pellets and faeces, since dispersal kernels and the potential for LDD are likely to differ between these forms of excreta (Proctor 1968, Sánchez et al. 2006), and regurgitation may be more likely for larger seeds (Kleyheeg and van Leeuwen 2015). Finally, we explored potential seasonal differences between spring and autumn migration in the number of seeds in excreta, as this will influence the directionality of LDD events.

Material and methods

Excreta samples were collected in Spain, Britain (NW England), Ireland and Iceland (Fig. 1, Table 1). In spring 2005, fresh faecal and pellet samples were collected in

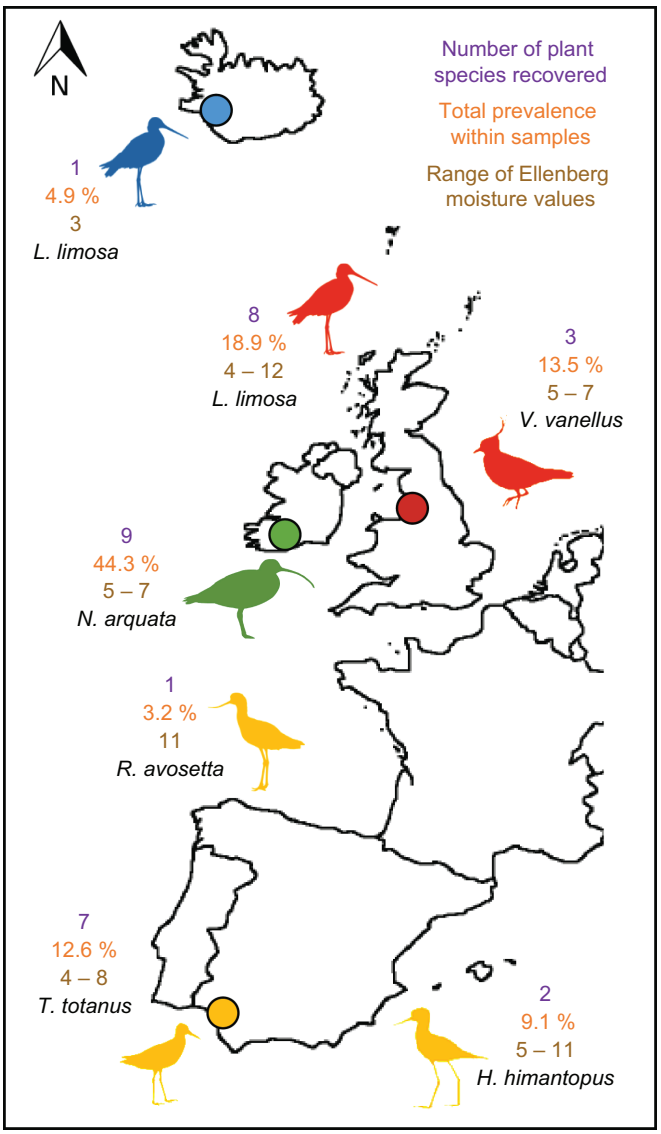

Figure 1. Summary of study locations and shorebird species, together with the number of plant species recorded in each study population, the prevalence of intact plant diaspores in excreta samples, and the habitat requirements of plant species (Ellenberg moisture F values of 1 to 4 are dry-soil terrestrial, 5 to 8 are moist-soil terrestrial, and 9 to 12 are aquatic plants). Each sample only represents a small fraction of the daily excreta output for a single bird.

solar salt ponds at Sanlúcar de Barrameda in Doñana Natural Park, Cadiz province, south-west Spain (36.834°N, 6.342°W). We sampled common redshank *Tringa totanus*, black-winged stilt *Himantopus himantopus* and pied avocet *Recurvirostra avosetta*. These birds were likely to have been feeding in and around the hypersaline ponds located within the delta of the Guadalquivir river (see Rendon et al. 2008 for details).

In 2016, we collected fresh excreta samples in Britain, Ireland and Iceland from three additional species (Table 1): northern lapwing *Vanellus vanellus*, Eurasian curlew *Numenius arquata* and Icelandic black-tailed godwit *Limosa limosa*, henceforth 'godwit'. In Britain, faecal samples were collected from lapwings feeding in pasture alongside an inland freshwater lake (53.289°N, 2.520°W). Godwit samples (Fig. 2) were collected from a small farm pond where several hundred birds roosted at high tide (53.380°N, 3.166°W), 2 km away from tidal mudflats in the Dee Estuary, which were their main feeding area (Supplementary material Appendix 3). These godwits were first sampled in late April, within two days of their departure to their breeding area in Iceland (Supplementary material Appendix 4). They were sampled again in August, less than a week after the arrival of the first sizeable flock from Iceland and when birds were still arriving, and again in September, over a month after their return and before many of them departed for wintering areas in other parts of Britain (Table 1, Supplementary material Appendix 4).

This same godwit population was also sampled in south Iceland during the same year, in the first half of May at a marsh pond where arriving birds roost (63.859°N, 20.256°W; Gunnarsholt), and in the second half of July in a freshly mowed hayfield (63.829°N, 20.987°W; west of Stokkseyri) where departure flocks congregate and prepare for the migratory flight from the breeding grounds to Britain.

In Ireland, faecal and pellet samples were collected from curlew roosting sites on raised grass embankments overlooking the edge of tidal mudflats at the Douglas Estuary, Cork (51.882°N, 8.434°W), in late July.

When sampling, we looked for resting monospecific flocks of shorebirds and sampled fresh faeces or pellets after the birds had flown away, paying attention to leave at least 1 m between the samples to minimize the risk of repeated sampling of the same individual (each faecal sample was only a small fraction of daily faecal output, see Results). The samples were individually checked for contamination with soil or wind-blown diaspores in the field, lifted off the substrate with a clean penknife, placed in plastic zip-lock bags, paper envelopes or plastic tubes, and then either air dried or kept in a fridge (4°C) until processing. In Spain, soil samples were also collected from spots adjacent to those with excreta, to assess the possibility of contamination of excreta with additional diaspores by soil contact. The mass of each sample from Britain and Ireland was measured before processing. Additional samples were weighed fresh and again after drying to relate fresh to dry mass. The separation of plant diaspores was done by washing the samples with deionized water on a 100 µm sieve. Only intact diaspores ('seeds' from hereon) were collected. Identification was done under a stereo-microscope by comparing the morphological traits (shape, size, colour and seed coat pattern) of seeds with available literature (Bojnanský and Fargašová 2007, Cappers et al. 2012; <www.brc.ac.uk/plantatlas/>). Species were identified as native or aliens (Supplementary material Appendix 1).

Table 1. Details of excreta samples collected from six different shorebird species and four countries (see also Fig. 1).

Species	Location	Date	N pellet samples	N faeces samples
Tringa totanus	Sanlúcar de Barrameda, Spain	27 April 2005	76	19
Tringa totanus	Sanlúcar de Barrameda, Spain	18 May 2005	16	–
Recurvirostra avosetta	Sanlúcar de Barrameda, Spain	27 April 2005	–	6
Recurvirostra avosetta	Sanlúcar de Barrameda, Spain	19 May 2005	–	25
Himantopus himantopus	Sanlúcar de Barrameda, Spain	27 April 2005	–	22
Vanellus vanellus	Budworth Mere, England	14 July 2016	–	37
Numenius arquata	Cork, Ireland	8 July 2016	32	8
Numenius arquata	Cork, Ireland	26 July 2016	14	7
Limosa limosa	West Kirby, England	29 April 2016	–	30
Limosa limosa	West Kirby, England	2 August 2016	–	40
Limosa limosa	West Kirby, England	16 September 2016	–	36
Limosa limosa	Gunnarsholt, Iceland	14 May 2016	–	21
Limosa limosa	Stokkseyri, Iceland	18 July 2016	–	20
Total			138	271

For the identified plant species, we extracted their morphological dispersal syndrome (i.e. the assumed means of dispersal) from the Baseflor database (Julve 1998). As an indication of habitat moisture requirements, we extracted the Ellenberg F indicator for angiosperm species from Julve (1998) and Hill et al. (1999) to assess the extent to which the birds were dispersing aquatic plants. Increasing moisture from wet to inundated conditions is represented by higher Ellenberg F values, and we considered plants with values of 1 to 4 to be dry soil terrestrial, 5 to 8 to be moist soil terrestrial, and 9 to 12 to be aquatic. Ellenberg F values were not available for one angiosperm species. For the charophytes we assigned a value of 12.

Spanish samples were collected during a study focused mainly on endozoochory of brine shrimp *Artemia* eggs (Sánchez et al. 2007), and no attempts were made to germinate the seeds extracted. Germinability tests were conducted for seeds collected in other countries. We used Petri-dishes filled with bacteriological agar placed on a laboratory window sill (selected British samples only), or in a germination chamber (Irish, Icelandic and remaining British samples) set on a cycle of 12 h light at 24°C and 12 h darkness at 18°C. Seeds were checked daily for germination for two months.

Figure 2. Black-tailed godwit faeces at a roost site in the Wirral, England.

Statistical analyses

While both pellets and faeces were collected for curlew and redshank, only faecal samples were collected for other species (Table 1). We tested the difference in number of diaspores and their length between sample types for curlew and redshank with generalized linear models (GLMs) in the R statistical environment (ver. 3.4.0, R Core Team). For the curlew model of number of diaspores, we used a negative binomial error distribution using the glm.nb function in the 'MASS' package (Venables and Ripley 2002). For the redshank model of number of diaspores, we applied a zero-inflated negative binomial model using the zeroinlf function in the 'pscl' package (Zeileis et al. 2008), due to the predominance of zero values for this species. For each sample with at least one intact diaspore, we calculated their overall mean length. We log transformed the mean length value and fitted it to a GLM with a normal error distribution, using the 'stats' package (ver. 3.4.0, R Core Team).

Godwits were particularly well sampled in Britain over time, covering three different months, and spring and autumn migrations at the same site (Table 1, Supplementary material Appendix 4). We therefore conducted further in-depth analyses of these data. Differences between months in the number of diaspores recovered per sample (while controlling for mass) were analyzed with a GLM with a negative binomial error distribution, using the glm.nb function in the 'MASS' package (Venables and Ripley 2002). For samples with at least one diaspore, the variation between months in the species composition of the diaspores was analysed with non-parametric permutational ANOVA (i.e. PERMANOVA; Anderson 2001), using the adonis function of the 'vegan' R package. This analysis was based on a Bray–Curtis dissimilarity matrix, composed of values between 0 and 1, reflecting the degree of dissimilarity among months. These analyses amount to an

assessment of the differences in plant community compositional centroids among months.

Data deposition

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.3b333s8> (Lovas-Kiss et al. 2018c).

Results

We collected 409 excreta samples (138 pellets and 271 faeces) from six different shorebird species and seven populations (Fig. 1); these contained 166 intact diaspores, with 164 angiosperm seeds and two charophyte oogonia. All bird populations had intact diaspores in their excreta, with 1–9 plant species recorded in each population (Fig. 1). We identified 27 plant taxa including 24 species, one taxon identified to genus and two to family level (Table 2, 3). Altogether, diaspores were recorded from 13 plant families. Overall, 13% of excreta samples (11% of faecal samples and 17% of pellets) contained at least one intact diaspore, and the prevalence for each population ranged from 3.2% in avocets to 44.3% in curlews (Fig. 1). We calculated a mean ratio between wet and dry mass for shorebird faeces (n = 19) of 3.37 + 0.32 (± SE). Godwits produce 1.97 g dry mass of faeces a day (data from Santiago-Quesada et al. 2009), which is equivalent to ca 6.65 g wet mass a day. The wet mass of fresh, godwit samples (n = 106) from the UK was 1.14 g ± 0.05 (mean ± SE). This suggests each of our samples contained ca 17% of daily faecal output.

Dispersal syndromes based on diaspore morphology did not predict which plant species were dispersed by endozoochory. Only four of the 22 species were assigned to the endozoochory dispersal syndrome, compared to six for anemochory (wind dispersal), five for barochory (self-dispersal), five for epizoochory and two for hydrochory (water dispersal: Table 2, 3). In terms of numbers of diaspores, epizoochory and anemochory were the most frequent syndromes (Fig. 3a). Of 23 species with Ellenberg F values, only three were aquatic whereas 20 were terrestrial (Table 2, 3). Of all intact seeds (Fig. 3b, n = 164), 86.6% were moist soil terrestrial (95% confidence intervals 80.5–91.0%), 2.4% were dry soil terrestrial (CIs 1.0–6.1%) and 10.9% were aquatic (CIs 7.1–16.7%). Aquatic plants were only recorded in three of seven bird populations (Fig. 1). In a given sample, the number of intact terrestrial seeds exceeded the number of aquatic seeds (Wilcoxon signed-rank test, n = 408, V = 243, $p < 0.0001$).

Spanish samples contained a total of 19 diaspores, representing five plant families and seven taxa (Fig. 1, Table 2). No diaspores were recorded in soil samples collected alongside excreta. For redshank, there was no significant difference between the number of diaspores in pellets and faecal samples (z-value = 0.075, p = 0.94), but the mean size of seeds found in pellets was significantly larger (t = 3.998, p = 0.001).

Table 2. Intact plant diaspores recovered from shorebird excreta in Doñana salt ponds, Spain. NS = N samples with taxon, TD = total diaspore number, Max = maximum number of diaspores in a given sample.

Plant family	Plant species	Dispersal syndrome*	Seed length (mm)	Ellenberg F**	*Tringa totanus* (n = 92 pellets)			*T. totanus* (n = 19 faeces)			*Recurvirostra avocetta* (n = 31 faeces)			*Himantopus himantopus* (n = 22 faeces)		
					TD	NS	Max	TD	NS	Max	TD	NS	Max	TD	NS	Max
Charophyceae	Unidentified		0.53[2]		–	–	–	2	2	1	–	–	–	–	–	–
Amaranthaceae	*Arthrocnemum macrostachyum*	hydrochory	1.24[2]	8	1	1	1	–	–	–	–	–	–	–	–	–
Asteraceae	*Crepis foetida*	anemochory	6.89[1]	4	1	1	1	–	–	–	–	–	–	–	–	–
	Sonchus asper	barochory	2.72[1]	5	1	1	1	–	–	–	–	–	–	–	–	–
	Sonchus oleraceus	barochory	2.84[1]	5	1	1	1	–	–	–	–	–	–	1	1	1
Fabaceae	*Trifolium repens*	epizoochory	1.28[1]	5	1	1	1	–	–	–	–	–	–	–	–	–
Ruppiaceae	*Ruppia* cf. *maritima*	hydrochory	3.13[1]	11	9	7	2	–	–	–	1	1	1	1	1	1
	Total				14	12	2	2	2	1	1	1	1	2	2	1

*Baseflor (Julve 1998); [1]Cappers et al. 2012; [2]our measurements; **Hill et al. (1999) and Baseflor.

Table 3. Intact plant diaspores recovered from shorebird excreta in England and Ireland. NS=N samples with taxon, TD=Total diaspore number, Max=maximum number of diaspores in a given sample.

Plant family	Plant species	Dispersal syndrome*	Seed length (mm)**	Ellenberg F***	*Vanellus vanellus* (n=37 faeces)			*Numenius arquata* (n=46 pellets)			*N. arquata* (n=15 faeces)			*Limosa limosa* (April, n=30 faeces)			*L. limosa* (August, n=40 faeces)			*L. limosa* (September, n=36 faeces)		
					TD	NS	Max	TD	NS	Max	TD	NS	Max	TD	NS	Max	TD	NS	Max	TD	NS	Max
Asteraceae	*Bellis perennis*	anemochory	1.42	5	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Cotula coronopifolia[1]	anemochory	1.92	7	–	–	–	–	–	–	–	–	–	–	–	–	10	4	6	12	4	8
Betulaceae	*Betula pendula*	anemochory	3.2	5	–	–	–	2	2	1	–	–	–	–	–	–	–	–	–	–	–	–
Brassicaceae	*Lepidium didymum*[1]	anemochory	2.43	5	–	–	–	–	–	–	1	1	1	–	–	–	–	–	–	–	–	–
Caryophyllaceae	*Sagina apetala*	anemochory	0.33	4	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1	–	–	–
Fabaceae	*Trifolium repens*	epizoochory	1.28	5	–	–	–	–	–	–	–	–	–	1	1	1	–	–	–	–	–	–
Ranunculaceae	*Ranunculus repens*	epizoochory	3.95	7	–	–	–	2	1	2	–	–	–	–	–	–	–	–	–	–	–	–
Rosaceae	*Potentilla indica*[1]	endozoochory	1.26	ND	–	–	–	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–
	Prunus cerasifera[1]	endozoochory	14.02	5	–	–	–	2	2	1	–	–	–	–	–	–	–	–	–	–	–	–
	Rubus idaeus	endozoochory	2.78	5	–	–	–	10	4	4	12	2	11	–	–	–	–	–	–	–	–	–
	Rubus fruticosus agg.	endozoochory	3.08	6	–	–	–	–	–	–	1	1	1	–	–	–	–	–	–	–	–	–
Juncaceae	*Juncus bufonius*	epizoochory	0.44	7	2	2	1	–	–	–	–	–	–	2	1	2	48	3	45	4	1	4
Plantaginaceae	*Callitriche hermaphroditica*	ND	1.37	12	–	–	–	–	–	–	–	–	–	–	–	–	3	1	3	1	1	1
	Veronica catenata	barochory	0.64	10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1
	Plantago major	barochory	1.61	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1
Poaceae	*Festuca arundinacea*	epizoochory	4.09	6	–	–	–	14	7	7	7	4	2	–	–	–	–	–	–	–	–	–
	Poa annua	barochory	1.59	5	2	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Poa trivialis	barochory	1.58	6	–	–	–	1	1	1	2	1	2	–	–	–	–	–	–	–	–	–
	Poa sp.		1.23		–	–	–	–	–	–	–	–	–	–	–	–	1	1	1	–	–	–
	Total				5	5	1	32	12	7	23	5	11	3	2	2	63	8	45	19	4	8

*Baseflor (Julve 1998), **Cappers et al. 2012, LEDA traitbase (Kleyer et al. 2008) and our own measurements, [1]alien species in UK-Ireland, ***Hill et al. (1999) and Baseflor.

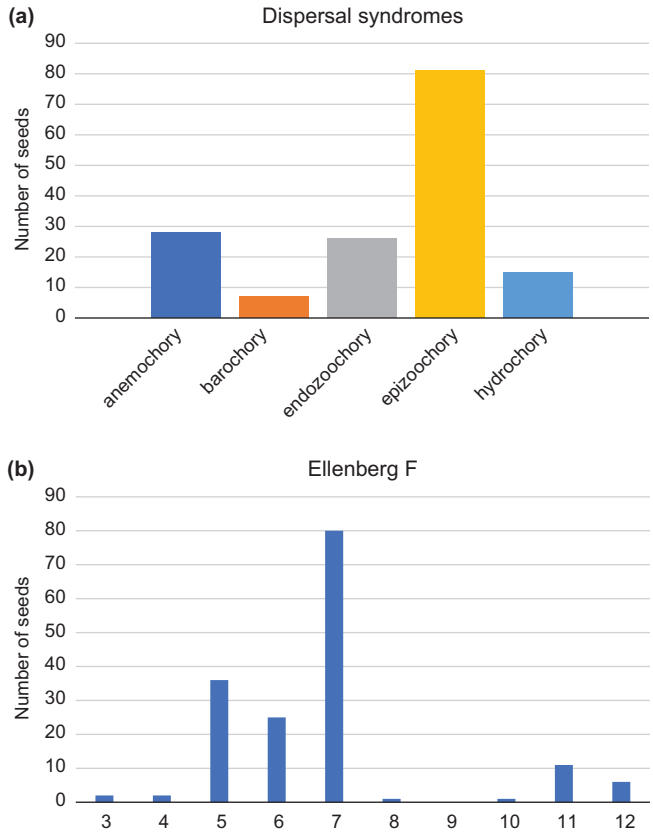

Figure 3. Total numbers of intact diaspores recorded according to: (a) dispersal syndromes from Baseflor. 9 additional seeds were from taxa of unknown syndromes. (b) Ellenberg moisture indicators. Increasing moisture from wet to inundated conditions is represented by higher Ellenberg F values. Plants with values of 1 to 4 are dry-soil terrestrial, 5 to 8 are moist-soil terrestrial, and 9 to 12 are aquatic. No seeds of values 1 or 2 were recorded. *Poa* sp. and *Potentilla indica* seeds were excluded, because they did not have an indicator value. See Table 2 and 3 for details.

In Britain and Ireland we found a total of 145 diaspores, representing ten families and 19 taxa (including 17 species, Fig. 1, Table 3). Four of the species were alien (Table 3). Six taxa (five species plus an unidentified *Poaceae*) germinated, including the alien buttonweed *Cotula coronopifolia* for which 44% of seeds germinated (Table 4). Seeds were germinated from the excreta of all three bird species, although success was lower for the curlew (Table 4). None of the plant taxa that germinated had an endozoochory syndrome. For the curlew, there was no significant difference between the number of diaspores in pellets and faecal samples (z-value = –1.089, p = 0.276), with a similar result when we controlled for sample mass (z-value = –0.856, p = 0.392). Similarly, we found no difference (t = 1.032, p = 0.318) in the mean length of diaspores between pellets and faecal samples. One pellet contained only styrofoam (polystyrene).

Godwit faeces from the UK site largely contained shell fragments as most feeding was conducted on tidal mudflats around low tide (Norman 2008). Seeds recovered from these samples may have been ingested at the roosting pond where some feeding was observed (Fig. 2, Supplementary material Appendix 3). When comparing the number of seeds found in godwit faeces between months (Table 3), there were significantly more seeds in August (z = 1.99, p = 0.04) and September (z = 2.10, p = 0.03) than in April, but no difference between August and September (z = 0.48, p = 0.63). There were no differences between months in the species composition of the seeds recovered ($F_{2,11} = 1.32$, p = 0.215).

In the case of Iceland, we found only one plant species *Cerastium nigrescens* (Caryophyllaceae, Fig. 1), which was represented by one intact seed each in two of the godwit samples from July (n = 20). Both seeds germinated during our tests.

Discussion

Six shorebird species in four different countries, spanning a wide latitudinal range, were found to be consistently dispersing a variety of plants by endozoochory. Importantly, these were mainly terrestrial flowering plants that do not have an 'endozoochory syndrome'. Thus, our findings do not support the view that waterbirds are only important as vectors of aquatic plants, nor the view that fruit and seed morphology allows an effective a priori prediction of which plants

Table 4. Results of germination trials for seeds recovered from shorebird excreta in England and Ireland, TD = total number of diaspores tested, NG = number of germinated diaspores. No seeds of other plants listed in Table 3 germinated.

		Vanellus vanellus (n = 37 faeces)		*Numenius arquata* (n = 46 pellets)		*Numenius arquata* (n = 15 faeces)		*Limosa limosa* (n = 106 faeces)		Total	
Plant family	Plant species	TD	NG	TD	NG	TD	NG	TD	NG	TD	NG
Asteraceae	*Bellis perennis*	1	1	–	–	–	–	–	–	1	1
	Cotula coronopifolia[1]	–	–	–	–	–	–	22	10	22	10
Juncaceae	*Juncus bufonius*	2	2	–	–	–	–	54	3	56	5
Plantaginaceae	*Callitriche hermaphroditica*	–	–	–	–	–	–	4	2	4	2
Poaceae	*Poa annua*	2	1	–	–	–	–	–	–	2	1
	Poa trivialis	–	–	1	1	2	0	–	–	3	1
	Total	5	4	1	1	2	0	80	15	88	20

[1]Alien species in UK-Ireland.

they disperse. Our study is unique in its broad spatial scale and in the large sample size, compared with the few previous assessments of endozoochory by shorebirds (Sánchez et al. 2006, Green et al. 2013). These data provide evidence that endozoochory can be an important mechanism of LDD for many plants whose seeds are not currently characterised as 'dispersed by animals', because they lack a fleshy-fruit.

Dispersal syndromes fail to predict endozoochory

Clearly, existing 'dispersal syndromes' are not adequate for describing the dispersal mechanisms of many plants. Endozoochory by vertebrates provides a greater median and maximum dispersal distance than other plant dispersal mechanisms (Bullock et al. 2017), and shorebirds particularly so (Viana et al. 2013). Although Higgins et al. (2003) recognized that LDD events are often due to 'nonstandard' dispersal mechanisms, rather than those predicted by dispersal syndromes, they did not propose endozoochory as one such atypical mechanism. Accordingly, the importance of endozoochory by many birds, including shorebirds, has been overlooked (see also Soons et al. 2016).

Seven of ten plant species recovered from samples collected in England or Iceland were germinated in the laboratory, and none of these had an 'endozoochory syndrome'. In contrast, eight of nine species recorded in the Irish curlew samples failed to germinate, including the four species with an endozoochory syndrome. Germination may have been poorer for the curlew because of a longer delay between excreta collection and processing, during which samples were transported between different countries. However, our data suggest the curlew is more frugivorous than the other shorebirds studied, supporting diet literature (Ridley 1930, Cramp and Simmons 1983).

Our results from different bird species and localities consistently show that shorebirds can be vectors for a wide range of plant species, and that known morphological dispersal syndromes do not accurately predict dispersal mechanisms. This suggests that Proctor (who emphasized endozoochory) was more correct than his contemporary Cruden (1966), who suggested that epizoochory by shorebirds was more important for colonization of oceanic islands by plants, or for the establishment of disjunct plant distributions split between the two hemispheres. Our work contradicts that of Schenk and Saunders (2017), who dismissed the importance of endozoochory and assumed that dispersal syndromes actually determine the mechanisms by which different plant species achieved disjunct distributions. Since their morphological inspections of diaspores indicated that the endozoochory syndrome is rare amongst disjunct plant species, they concluded that endozoochory per se is rare. On the contrary, our field data show that endozoochory by shorebirds is a regular event for plants assigned to epizoochory, anemochory or other syndromes, and that these seeds often remain viable after gut passage.

Importantly, plant dispersal syndromes are generally assigned in the absence of field data on dispersal mechanisms (Heleno and Vargas 2015, Schenk and Saunders 2017). Hence, syndromes do not necessarily reflect even the most frequent in situ dispersal mechanisms. Furthermore, when their diaspores are inspected, a high proportion of plants are not considered to have 'obvious adaptations' for a dispersal mechanism, and are variously categorized as 'unspecialized' or 'self-dispersed' (e.g. barochory according to Julve 1998). Heleno and Vargas (2015) found that 63% of both the European flora and the flora of the Azore islands have unspecialized diaspores, and that dispersal syndromes do not readily explain the colonization of oceanic islands by plants. This may partly be due to the failure of syndromes to predict endozoochory by migratory waterbirds.

Some authors have argued that endozoochorous LDD by shorebirds is likely to explain bipolar and other disjunct distributions of fleshy-fruited plants (Popp et al. 2011, Schenk and Saunders 2017). However, our results show that endozoochory by shorebirds can occur for a much broader range of terrestrial and aquatic plants. Currently, however, the taxonomic diversity of plants dispersed by shorebirds is unclear pending further studies such as ours. Diet studies suggest numerous angiosperms are dispersed by shorebirds (Green et al. 2002). So far, more information is available for migratory dabbling ducks, which disperse hundreds of angiosperm species within Europe, representing a broad range of life-histories and habitat types (Soons et al. 2016, Lovas-Kiss et al. 2018a). Like ducks, shorebirds are also likely to disperse mosses and other non-flowering plants (Wilkinson et al. 2017).

Relationship between plant distributions and shorebird flyways

The distributions of the plant taxa we recorded and of shorebird flyways are consistent with a potential role of shorebirds in the LDD of these plants (Supplementary material Appendix 1, 2). Following Darwin's logic in our paper's epigraph concerning aquatic plants, the widespread distribution of these terrestrial plants may be partly due to their dispersal by waterbirds (see also Brochet et al. 2009). All but one of the plant taxa recorded have broad latitudinal distributions, and are recorded in at least two of the three geographical areas (Iceland; Britain/Ireland; Spain) included in our study (Supplementary material Appendix 1). The exception is the glasswort *Arthrocnemum macrostachyum* (Chenopodiaceae), which is widespread longitudinally in the Mediterranean region and the Middle East, where stilts and avocets are likely vectors given their movement patterns (Delany et al. 2009). We observed little overlap between plant taxa recorded in excreta from Spain, England, Ireland or Iceland, largely because we sampled different habitat types in each country. The only exception was white clover *Trifolium repens*, recorded in both Spain and England. In a previous study of endozoochory by redshank and godwits, in different salt ponds 60 km from our Spanish study site, two plant species we documented (*A. macrostachyum* and *Sonchus oleraceus*) were similarly recorded (Sánchez et al. 2006).

Population genetics of the plant taxa recorded are also consistent with LDD events by birds (Palmé et al. 2003, Martinez-Garrido et al. 2017).

Five of the six shorebird species share large, migratory populations with a common flyway (the East Atlantic Flyway) covering at least two out of the three geographical areas (Wernham et al. 2002, Delany et al. 2009, Supplementary material Appendix 2). The exception is the stilt, which has more potential as a circum-Mediterranean vector, but even this species often moves from southern Spain to the UK (Figuerola 2007). The godwit has a common flyway expanding from Iceland into the Iberian Peninsula and beyond into north-west Africa. The redshank also covers our entire study area, split between two flyways (Supplementary material Appendix 2). Thus, both godwits and redshanks have the potential to disperse plants across the latitudinal range from 36° to 64°N.

LDD by migratory waterbirds is likely to be particularly important, given the need for native plants to move northwards so as to keep pace with climate change (Corlett and Westcott 2013, Viana 2017). It may also play a key role in the rapid spread of alien plants introduced into Europe (Green 2016). Modelling (Viana et al. 2013) supports Proctor's (1968) view that, compared with larger waterbirds such as ducks, geese and swans (Anatidae), shorebirds have particularly long maximum gut retention times that are ideal for LDD events. Some shorebirds undergoing extremely long migrations (much farther than the distance between the UK and Iceland) have been found to atrophy their guts before departure (Piersma 1998) which is likely to reduce the chance of endozoochory. However, there is no evidence for this in our study populations, and icelandic godwits continue feeding right up to departure (Alves et al. 2012). As well as during migratory flights, shorebirds can disperse plants during daily movements while at breeding sites, stopover sites or during winter, when they can move 10–20 km or more during daily movements between roosts and feeding sites (Dias et al. 2006, Taft et al. 2008). Accordingly, shorebirds can readily connect different patches in a plant metapopulation and provide an ecosystem service through plant dispersal (Green and Elmberg 2014), emphasising the need to conserve those shorebird populations currently in decline (Sutherland et al. 2012, Pearce-Higgins et al. 2017).

Buttonweed, an alien spread by waterbirds?

We found shorebirds to disperse three plant species alien to Europe and another eight alien to part of the study area (Supplementary material Appendix 1). For example, we found that godwits disperse the buttonweed *Cotula coronopifolia*, which is native to South Africa and is highly invasive in its non-native range (Nentwig et al. 2017). Indeed, almost 90 yr ago Ridley (1930) speculated that the widespread distribution of *C. coronopifolia* may be partly due to epizoochory by shorebirds. This plant is already present in fourteen countries in Europe (<www.europe-aliens.org>), North and South America, Australia and New Zealand, and is spreading rapidly across the UK and coastal areas of the Iberian Peninsula (Costa et al. 2009, Vilà et al. 2012). Godwits may be important vectors for this plant, given their migratory behaviour and the high germinability of seeds in faeces (Table 4), and may have introduced it to our sampling site where this plant was common (Supplementary material Appendix 3). During migration, several thousand *L. limosa* (<www.rspb.org.uk/birds-and-wildlife/wildlife-guides/bird-a-z/black-tailed-godwit>) travel across the United Kingdom passing through suitable habitats for the buttonweed (Wernham et al. 2002, Alves et al. 2010, <www.brc.ac.uk/plantatlas/>). However, this bird may not be the most important avian vector for *C. coronopifolia*, since seeds are eaten by ducks in Australia and North America (Raulings et al. 2011, Casazza et al. 2012). van Der Toorn (1980) also suggested that greylag geese *Anser anser* may have a role in its spread in northern Europe.

Importance of other animal vectors

Although our data are consistent with a role for shorebirds as plant vectors, are other animal vectors more important for endozoochory? A review of literature and of plant databases showed that no other animal vectors have been reported for five of the 24 angiosperm species, whereas domestic and wild ungulates were reported for 12 species (Supplementary material Appendix 5). Although ungulates are likely to move more seeds within a landscape, migratory waterbirds undoubtedly provide a much greater maximum dispersal distance and the capacity to disperse seeds between land masses. Seeds of ten of the plant species have also been reported in the gut contents of dabbling ducks from Europe (largely ingesta data without quantifying prevalence or viability in excreta, Soons et al. 2016), and the absence of the other species might reflect the general shortage of studies of endozoochory by waterbirds. Empirical data are too few for us to rule out the possibility that ducks, geese or other waterbirds are more important for the LDD of these plants in Europe than shorebirds. Similarly, it is difficult to compare the prevalence of seeds in our samples with data for other vectors, owing to a shortage of studies that quantify prevalence. In a recent mallard study during autumn migration, intact diaspores were found in 32% of faecal samples (Lovas-Kiss et al. 2018a, b). In a study of Arctic geese outside migratory periods, they were found in 78% of faecal samples (Green et al. 2018).

Seasonality of dispersal potential

There was no obvious latitudinal trend in the prevalence of seeds in shorebird excreta (Fig. 1), but we recorded a seasonal difference in the number of seeds found in faeces at a UK passage site, from which godwits migrate both to and from Iceland, with fewer seeds recorded during spring migration. Clausen et al. (2002) speculated that a seasonal effect existed for endozoochory by Anatidae migrating in northern Europe, in relation to the timing of seed production. However, Sánchez et al. 2006 found the opposite result in

southern Spain, with more seeds in redshank pellets in spring than in autumn. This contrast may be related to the timing of seed production, which generally is much earlier at lower latitudes. The probability of a northwards LDD event during spring migratory movements may perhaps decrease as the latitude of the departure location increases. However, this topic requires further in-depth research. Spring migration is particularly important because it allows plants to shift their distribution northwards in response to climate change. Research on plant dispersal by migratory ducks in southern Europe has revealed similar rates of seed transport in autumn and spring (Figuerola et al. 2003, Brochet et al. 2010). Notably, all plant species recorded in godwit faeces in spring in Britain, or in summer in Iceland, are present in both countries (Supplementary material Appendix 1), which is consistent with a role for shorebirds as LDD vectors. Equally, five of the six plant species recorded in Britain in August–September are present in southern Spain, within the godwit wintering range (Supplementary material Appendix 1).

Seed size and the potential for endozoochory

We had expected to find bigger seeds in pellets, as larger food items tend to be regurgitated more readily (Sánchez et al. 2005). Equally, larger seeds are less likely to survive gut passage to faeces in a viable condition in Anatidae (Green et al. 2016). Very large seeds (e.g. ca > 5 mm) can only leave the gizzard by regurgitation, as they cannot pass into the intestines unless they are broken into smaller pieces. Our finding for redshank that larger seeds are egested in pellets suggests the potential for dispersal by endozoochory is not as limited by seed size as it would otherwise be. However, one of the largest and hardest seeds we recorded were stones of *Rubus idaeus* (length: 2.78 mm, width: 1.62 mm), whose abundance in curlews did not differ between pellets and faeces (z-value = –0.98, p = 0.32). LDD events are more likely when retention times are longer, and Proctor (1968) found that maximum retention times for seeds in captive shorebirds were longer for pellets. In contrast, in the yellow-legged gull *Larus cachinnans*, seeds egested in faeces had longer mean retention times than those in pellets (Nogales et al. 2001). This difference might be related to a higher frequency of pellet production in gulls than shorebirds. Inactive birds in captivity are also likely to have different retention times to those in the wild, although retention time and seed survival for ducks may be under-estimated in captive studies (Kleyheeg et al. 2015).

Conclusions

Endozoochory by shorebirds is a means of dispersal for a wide variety of aquatic and especially terrestrial plants, which is not correctly accounted for by assigned dispersal syndromes. Accordingly, greater consideration of shorebirds as plant vectors is required in biogeographical studies, and in attempts to predict maximum dispersal distances, which in turn partly determine how plants spread (Tamme et al. 2014). More empirical work is needed to establish which plants are dispersed by shorebirds, and other waterbirds, and in what direction, and whether there are plant traits (e.g. phenology, seed shape, size and hardness) that allow us to make a priori predictions. Such advances in research are necessary if we are to better understand what dispersal mechanisms underlie the colonization of oceanic islands, or the establishment of disjunct (e.g. bipolar) distributions. Furthermore, once we have identified plants dispersed by waterbirds, we will be able to improve models of how their distributions will respond to climate change, or to predict the advance of problematic alien species (Viana 2017).

Our study illustrates how migratory waterbirds are important to maintain connectivity between plant communities at broad scales (Amezaga et al. 2002). There is growing concern about the conservation of migratory shorebird populations, many of which are in decline (Pearce-Higgins et al. 2017) and/or are rapidly changing their migration patterns (Godet et al. 2011). Through seed dispersal, shorebird conservation will help maintain biodiversity and ecological function in a rapidly changing world.

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Supplementary material (Appendix ECOG-04065 at <www.ecography.org/appendix/ecog-04065>). Appendix 1–5.