



Migratory geese allow plants to disperse to cooler latitudes across the ocean

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Abstract

Aim: How plants can disperse in response to global change is a critical question, yet major knowledge gaps persist about long-distance dispersal (LDD) mechanisms. We studied the potential a migratory waterfowl has for LDD of flowering plants via gut passage of seeds (endozoochory), comparing spring and autumn migration.

Location: United Kingdom and Iceland.

Taxon: Pink-footed Goose (*Anser brachyrhynchus*, Baillon) and Angiosperma.

Methods: We studied endozoochory by Pink-footed geese migrating within and between the UK and Iceland by faecal sampling and GPS tracking. We collected 614 faecal samples from 14 areas in the UK and one in Iceland. Using GPS tracks to and from these areas, we estimated how far seeds can be dispersed by Pink-footed geese, and where to or from.

Results: We recorded 5507 intact seeds of 35 species (27 terrestrial) from 15 plant families, with lower seed abundance per dropping when birds were migrating northwards in the UK during spring than upon their arrival in autumn. Species richness of plant seeds was highest in Iceland and in autumn. Only four plant species dispersed had an “endozoochory syndrome”. GPS movements showed that seeds retained in guts for up to 24 h can be readily dispersed in both directions between the UK and Iceland, with maximum distances exceeding 2000 km, as well as between UK localities

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separated by 100s of km. Movements northwards of ≤ 400 km were even recorded in autumn. While at stopover sites, daily movements between roost and feeding sites often exceed 20 km.

Main Conclusions: Pink-footed geese are LDD vectors for plants previously assumed to lack an LDD mechanism. Spring migration is not the only period when geese move plants to cooler latitudes. The pink-footed goose can allow terrestrial and aquatic plants to cross the ocean and to keep pace with climate change.

KEYWORDS

endozoochory, island biogeography, long-distance dispersal, migration, pink-footed goose, seed dispersal, waterfowl

1 | INTRODUCTION

Seed dispersal is an important ecological process with a long history of research (Green et al., 2016; Ridley, 1930). Long-distance dispersal (LDD) is particularly important in the face of global change, yet major knowledge gaps persist about mechanisms. LDD has allowed plants to change their distributions in the geologically recent past in response to glacial/interglacial cycles (Huntley & Webb, 1989; Reid, 1899), but given the speed of ongoing climate change it is unclear if plants have adequate LDD mechanisms to keep pace. In general, seed dispersal by animal vectors, whether by gut transport (endozoochory) or external attachment (epizoochory), provide greater maximum dispersal distances than other seed dispersal mechanisms, including wind (anemochory) and water (hydrochory; Bullock et al., 2017; Wilkinson, 1997). Migratory birds can provide the largest LDD and move plants between land masses (Viana et al., 2016), making it imperative to improve our understanding of which plants they can disperse, especially during migration (González-Varo et al., 2021).

Under the dominant paradigm, dispersal mechanisms are predicted from morphology (i.e. morphological dispersal syndromes), and only plants with a fleshy fruit are assumed to disperse by endozoochory (Green et al., 2022). A mis-match between the timing of fruit availability and the spring migration of frugivorous birds severely limits the potential of angiosperms to disperse to cooler latitudes in response to global heating (González-Varo et al., 2021). However, there is increasing evidence that waterbirds and other non-frugivorous, migratory birds are major vectors by “non-classical endozoochory” of a broad range of plants that were previously assumed to lack an LDD mechanism (Green et al., 2016, 2022, 2023). These vectors include shorebirds (Lovas-Kiss et al., 2019), cormorants (van Leeuwen et al., 2017), herons (Navarro-Ramos et al., 2021) and gulls (Martín-Vélez et al., 2021), but migratory waterfowl (*Anatidae*) are particularly important given their abundance, widespread distributions and diets (Almeida et al., 2022; Green et al., 2016). Zoochory research on waterfowl has so far concentrated mainly on migratory dabbling ducks and other Anatini (Lovas-Kiss et al., 2018; Soons et al., 2016; Urgyán et al., 2023). These studies show that, contrary to common belief, waterfowl disperse many more seeds by endozoochory than by epizoochory (Green et al., 2016, 2023). Among

migratory waterfowl species, geese (*Anserini*) are often abundant, and can dominate waterbird biomass at temperate latitudes, especially during the breeding season in the sub-Arctic and Arctic (Buij et al., 2017). The few existing studies of their role in seed dispersal suggest geese are important vectors for a range of plants, most of which are terrestrial (Almeida et al., 2022).

Surprisingly, there are no previous studies of seed dispersal by geese during migration. The Pink-footed goose (*Anser brachyrhynchus*; PFG) is an abundant migratory species of interest for its potential dispersal of plants over long distances during its migration to breeding sites in the Arctic and sub-Arctic (Brides et al., 2020; Mitchell, 2002). Genetic and floristic studies are consistent with a major role for migratory geese in the LDD events that led to colonization by plants of North Atlantic Islands such as Iceland, including plants lacking morphological syndromes associated with zoochory (Alsos et al., 2015). In particular, these studies suggest dispersal consistent with PFG migration routes (Alsos et al., 2015), although there are no existing empirical studies of plant dispersal by this species. Feeding experiments with other goose species showed that some viable seeds are retained in their guts for at least three days—the mean retention time varied between 4 and 17 h (García-Álvarez et al., 2015; Reynolds & Cumming, 2016).

We sampled faeces from flocks of PFG in different habitats at different times of the year in the UK and Iceland with the aim of identifying plants dispersed by endozoochory during spring (northwards) and autumn (southwards) migration. We took advantage of tracking studies of migratory behaviour to locate flocks, and to understand the likely nature of seed LDD events. Our working hypotheses were as follows: (i) PFG disperse a greater abundance and diversity of seeds during autumn than spring migration, since fruiting generally occurs in late summer; (ii) the plant communities dispersed vary between seasons and habitats, due to variation in availability of diaspores and plant communities present; (iii) seeds from plants with an endozoochory syndrome are relatively more abundant in samples from autumn (when fleshy fruit production peaks), whereas plants with other syndromes are also dispersed in spring, as geese can ingest them inadvertently when drinking or feeding at ground level; (iv) moisture indicators of plants dispersed are consistent with habitats where faeces are collected (e.g. aquatic plants dominant in wetlands),

because most egested seeds are likely to be ingested in similar habitats; (v) PFG can disperse seeds between the UK and Iceland.

2 | MATERIALS AND METHODS

2.1 | Study species

The Greenlandic-Icelandic PFG population breeds in Iceland (where it is the most abundant goose species) and Greenland, and winters solely in Britain and Ireland, with a current population of around half a million (Mitchell, 2002; Wood et al., 2020). Autumn migration occurs mainly from early September until early October, and spring migration from mid-February until mid-May (Robinson, 2005). Within the UK, numbers have increased since 1960, and geese concentrate in Scotland, as well as east and northwest England, with most birds moving further south after their initial arrival as the winter progresses (Brides et al., 2020; Fox et al., 1994). Wintering PFG typically roost at night in aquatic habitats such as lakes, reservoirs or estuaries, and undertake daily flights to feed in surrounding agricultural fields (Devenish et al., 2015; Kear, 2005; Wood et al., 2020). Feeding sites may be up to 90 km away from roost sites, although they are usually within 5 km (Wood et al., 2020).

2.2 | Sample collection and processing

Faecal samples were collected from roosts and feeding sites in England (Lancashire and Norfolk), Scotland (south-west and central) and Iceland. Samples were collected over three years (2016–2018, Lovas-Kiss et al., 2023). Faecal sampling coincided with the tracking of migrating geese with GPS–GSM transmitters (see below). In particular, in April 2018, tracking data were used to locate passage sites used by flocks of geese in Scotland, which we then sampled. For details of localities and dates, see Table S1. In the UK, 199 samples were collected during spring migration (March or April), 382 during autumn migration (September or October), and 9 samples during winter (January). In Iceland, 25 samples were collected from a grazed grassland in September, during autumn migration.

The collection of faecal samples was from three main habitat categories in the UK: wetlands, improved pasture and arable. Wetland habitats included coastal and inland marshes. Arable were harvested agricultural fields (including cereal stubble and root crops). In one area (Martin Mere), faeces were sampled from both wetland and arable habitats. Large monospecific flocks containing hundreds of geese were located and, after they flew elsewhere, fresh faeces were collected by walking along transects through the habitat. Samples were separated by ≥ 2 m to avoid repeated collection from the same individuals. Each dropping was inspected to remove any soil or other items attached on the outside, then placed in a zip lock bag. Samples were placed in the fridge until seed separation. Some samples from wetlands (116)

were processed for propagules within three months after collection, but most samples (498) were refrigerated for 7–29 months until we had time to process them.

Samples were weighed (fresh mass) then washed in a 100 μ m sieve under tap water. Remaining material was examined under a stereomicroscope for intact diaspores ('seeds' from hereon). We considered a seed intact when it had no visible cracks. Seeds were identified using Bojnanský and Fargašová (2007), Cappers et al. (2012) and a personal seed herbarium. We retrieved fruit type and dispersal syndrome for each plant species from the BASEFLOR database (Julve, 1998), and Ellenberg F numbers (an indicator of moisture requirements) from Hill et al. (1999). We considered aquatic plants to have $F \geq 9$. Barochory syndrome suggests diaspores simply fall off the mother plant, and would be assigned when diaspores lack the features used to identify other syndromes (hooks, wings, fleshy fruit, etc). Germinability tests were carried out in Petri dishes with bacteriological agar on a laboratory window sill (samples processed within 3 months) or in a germination chamber (other samples) set on 16 h light at 25°C, 8 h darkness at 18°C. Seeds were checked daily for germination for one month. No seeds germinated from samples stored for ≥ 7 months before processing.

To analyse resulting seed dispersal data, we used four categories representing periods of the migratory cycle (spring UK [March–April], autumn UK [September–October], autumn Iceland [September] and winter UK [January]). We also used three habitat categories (wetland, pasture, arable).

2.3 | Tracking methods

A total of 73 GPS–GSM collars were fitted to female PFG (28 in Iceland, 45 in the UK) between December 2016 and July 2018, to study the impacts of wind-farms (details in Wood et al., 2020). Six were first winter females, all others were adults. Males were avoided to prevent marking paired birds that would move together. PFG were caught using cannon-nets in the UK (winters 2016/17 and 2017/18) or by rounding up flightless moulting geese in Iceland (July 2017 and 2018). They were fitted with plastic neck collars including an integral GPS–GSM unit and solar panel (Ecotone Telemetry; <http://www.ecotone.pl/>).

The GPS collars provided accurate location data, with an estimated latitude error of 15.6 m (0.63 m SE) and longitude error of 8.9 m (0.32 m SE; Wood et al., 2020). Location data were collected from the day after deployment to either the day before the GPS collar stopped working (or the bird was shot) or 31 May 2019, by which time any birds that were still alive had migrated north to Iceland. Number of location fixes was limited by battery power. For the data collected within the UK, a minimum of two fixes a day (normally at 00h00 and at 12h00) were available for 97.4% of the time (informing on where each goose roosted at night and fed at midday), and at least four location fixes a day (normally at 00h00, 06h00, 12h00 and 18h00) were available for 70.6% of the time (details in Wood et al., 2020).

All tagged birds arrived within the UK between 12 September and 27 October, and all left the UK between 28 March and 31 May to return to Iceland. Telemetry data are summarized at: <https://sites.google.com/view/telemetry/pinkfeet-2016-2019>.

In order to understand the nature of long-distance movements of geese likely to disperse the seeds found in our faecal samples, we filtered those geese whose tracks included fixes within 20 km of our exact sampling locations, and within 15 calendar days of our sampling dates (even if the year was different, for example applying movements from September 2017 to 2018 to sampling from 2017). This presents a conservative snapshot of the seed dispersal events to be expected from the large PFG population wintering in the UK, which utilizes a much larger number of sites than those we sampled. Because of the limited temporal resolution of the tracking data (often only 2 fixes a day), and because some seeds are likely to be retained in goose guts for up to 72 h (García-Álvarez et al., 2015), we concentrated our analysis on movements made by tracked geese up to 24 h before, and up to 24 h after, visiting the vicinity of our sample locations. In total, 20 individual tagged birds satisfied our criteria, and the number of individual birds passing close to a sampling location within the time frame for a given sampling event ($n=18$) ranged from 1 to 20 birds.

As we were interested in LDD events, we first extracted the maximum distance moved within 24 h before arrival to the area within 20 km of our sampling point, and after departing this area, for each individual and each sampling event (i.e. two measures of Haversine distance for each individual). We inspected manually the trajectories of each goose to exclude any individuals that may have overflowed the sampling area without stopping. We visualized movements to and from each area in separate maps for spring and autumn movements, using ArcMap 10.8. These movements simulate extreme seed LDD events to and from the sampling area with seed retention times of a maximum of up to 24 h. For each sampling event, we calculated the maximum and median movement distance based on the accumulated sum of Haversine distances between the first fix once the individual arrived at the site and the farthest fix in the previous 24 h period (arrival distance), as well as between the last fix at the site prior to departure and the farthest fix within the following 24 h period (departure distance). Importantly, the maximum displacement recorded was not necessarily the distance from the departure point after an interval of 24 h, since the maximum distance recorded for any fix during the 24 h period was sometimes after a shorter interval (e.g. 6 or 12 h after departure). Furthermore, since there were often only two fixes a day, the time taken for the movements we quantified was often likely to be much less than 24 h.

In between these departure and arrival flights, individual geese spent a number of days around the sampling area. However, they often made long distance daily movements of interest for seed dispersal, returning to the sampling area for part of the day. We mapped these intermediate movements in [Supporting Information](#), thus simulating additional seed LDD events.

2.4 | Statistical analysis

For analysis, we removed the winter category because of small faecal sample size ($N=9$), and our interest in migration periods. Variation in the composition of plant communities dispersed by endozoochory among migration periods and habitat types was tested using Generalized Linear Models for Multivariate Abundance Data (mvabund) with negative binomial error distribution and log link with an unknown overdispersion parameter, using the 'mvabund' v4.2.1 package in R (Wang et al., 2012). This analysis allows the identification of multivariate patterns and fitting of separate Generalized Linear Models (GLMs) for each dispersed plant species, using different explanatory variables. Using pairwise comparison shows the differences between each migratory period and habitat types. Resampling-based hypothesis testing within 'mvabund' was used to test which plant species were driving these multivariate abundance patterns (Wang et al., 2012).

To visualize the differences in dispersed communities between the migration period and habitats, we used a model-based approach using Bayesian Ordination and Regression Analysis (boral) latent-variable negative binomial models (Warton et al., 2015) with the 'boral' v2.0 package in R. We used default parameters for controlling the Markov Chain Monte Carlo (MCMC) sampling based on abundance data (including samples with no seeds) of species across communities (Hui, 2016). The mean of the posterior latent variable medians for each migration period and habitat were plotted in an ordination, where the first two axes represent the most important axes of species variation (Hui, 2016).

To analyse variation in prevalence of seeds (presence/absence: 1 = seeds, 0 = no seeds), we used generalized linear models (glmer) with binomial distribution from the package 'lme4' v1.1.33 (Bates et al., 2015), where the independent variables were habitat types or the migration period. Collection site was a random factor in all models, together with collection year for habitat type models. Rarefaction analysis was used to compare species richness found in samples collected from different countries and migration periods using the 'iNEXT' v3.0.0 (Chao et al., 2014) package.

To analyse differences among habitat types and migration periods for the total number of seeds, we used glmer with a negative-binomial distribution using the 'glmmTMB' v1.1.7 package (Brooks et al., 2017). We used collection site within the migration period and habitat type as independent variables, while collection year was also included as a random factor in the habitat type models. Similar models were used to analyse variation in the number of species per sample (excluding zeros). All statistical analyses were done in R v4.2.0 (R Core Team, 2022).

3 | RESULTS

From 614 fresh faecal samples we extracted 5507 intact seeds, from 35 terrestrial and aquatic plant species that represented 15 plant families, with moisture requirements ranging from dry to wet soils (Table 1). Only one of these species is restricted to Iceland (*Galium normanii*), whereas 10 are found in the UK but not Iceland. Of the

TABLE 1 Total number of intact diaspores (TD), number of samples with diaspores (NS) and maximum number of diaspores (Max) for 35 plant species recorded in faecal samples of pink-footed geese during migratory periods.

Plant family	Plant species	Ellenberg F	Fruit type	Dispersal syndrome	Spring UK (n = 208)			Autumn UK (n = 381)			Autumn Iceland (n = 25)		
					TD	NS	Max	TD	NS	Max	TD	NS	Max
Amaranthaceae	<i>Salicornia ramosissima</i> J.Woods ^{a,f}	7	-	-	-	-	28	2	26	-	-	-	
Asteraceae	<i>Tanacetum vulgare</i> L. ^{a,e}	6	Achene	Anemochory	-	-	1	1	1	-	-	-	
Boraginaceae	<i>Myosotis scorpioides</i> L. ^{a,e}	9	Achene	Barochory	-	-	1	1	1	-	-	-	
Cyperaceae	<i>Carex chordorrhiza</i> L. ^{a,d}	9	Achene	Hydrochory	-	-	-	-	-	80	3	70	
	<i>Eleocharis palustris</i> (L.) Roem. & Schult. ^{a,d}	10	Achene	Epizoochory	-	-	2	2	1	-	-	-	
Ericaceae	<i>Calluna vulgaris</i> (L.) Hull ^{a,d}	6	Capsule	Anemochory	-	-	1	1	1	-	-	-	
	<i>Empetrum nigrum</i> L. ^{a,d}	6	Berry	Endozoochory	-	-	349	18	147	883	18	365	
	<i>Vaccinium myrtillus</i> L. ^{a,d}	6	Berry	Endozoochory	-	-	-	-	-	411	10	90	
	<i>Vaccinium oxycoccos</i> L. ^{a,d}	9	Berry	Endozoochory	-	-	-	-	-	3	2	2	
	<i>Vaccinium uliginosum</i> L. ^{a,d}	6	Berry	Endozoochory	-	-	-	-	-	4	1	4	
Fabaceae	<i>Lotus corniculatus</i> L. ^{a,e}	4	Pod	Barochory	-	-	1	1	1	-	-	-	
Juncaceae	<i>Juncus acutiflorus</i> Ehrh. ex Hoffm. ^{a,f}	8	Capsule	Epizoochory	-	-	20	4	15	-	-	-	
	<i>Juncus articulatus</i> L. ^{a,d}	9	Capsule	Epizoochory	-	-	3271	3	3264	-	-	-	
	<i>Juncus bufonius</i> L. ^{a,d}	7	Capsule	Epizoochory	1	1	1	32	4	25	-	-	
	<i>Juncus compressus</i> Jacq. ^{a,f}	8	Capsule	Epizoochory	-	-	20	1	20	-	-	-	
	<i>Juncus effusus</i> L. ^{a,f}	7	Capsule	Epizoochory	4	3	2	3	2	2	-	-	
	<i>Juncus gerardii</i> Loisel. ^{a,d}	7	Capsule	Epizoochory	33	7	17	-	-	-	-	-	
	<i>Juncus triglumis</i> L. ^{a,d}	9	Capsule	Epizoochory	-	-	-	-	-	230	3	156	
Plantaginaceae	<i>Plantago major</i> L. ^{a,d}	5	Achene	Barochory	-	-	2	1	2	-	-	-	
	<i>Plantago media</i> L. ^{a,f}	4	Achene	Barochory	-	-	2	1	2	-	-	-	
Poaceae	<i>Brachypodium sylvaticum</i> (Huds.) P.Beauv. ^{a,f}	5	Caryopsis	Epizoochory	-	-	1	1	1	-	-	-	
	<i>Bromus ramosus</i> Huds. ^{a,f}	6	Caryopsis	Epizoochory	-	-	1	1	1	-	-	-	
	<i>Hordeum vulgare</i> L. ^{b,e}	4	Caryopsis	Epizoochory	-	-	1	1	1	-	-	-	
	<i>Poa annua</i> L. ^{a,d}	5	Caryopsis	Barochory	-	-	81	16	21	-	-	-	
	<i>Poa pratensis</i> L. ^{a,d}	5	Caryopsis	Barochory	1	1	1	1	1	-	-	-	
Polygonaceae	<i>Polygonum aviculare</i> L. ^{a,d}	5	Achene	Barochory	-	-	11	1	11	-	-	-	
	<i>Bistorta vivipara</i> (L.) Delarbre ^{a,d}	6	Achene	Barochory	-	-	-	-	-	1	1	1	
Ranunculaceae	<i>Ranunculus acris</i> L. ^{a,e}	6	Achene	Epizoochory	1	1	1	-	-	-	-	-	
	<i>Ranunculus aquatilis</i> L. ^{a,f}	10	Achene	Hydrochory	-	-	16	2	15	-	-	-	
	<i>Ranunculus sceleratus</i> L. ^{a,f}	8	Achene	Hydrochory	-	-	3	1	3	-	-	-	

TABLE 1 (Continued)

Plant family	Plant species	Ellenberg F	Fruit type	Dispersal syndrome	Spring UK (n = 208)			Autumn UK (n = 381)			Autumn Iceland (n = 25)		
					TD	NS	Max	TD	NS	Max	TD	NS	Max
Rosaceae	<i>Potentilla anserina</i> L. ^{a,d}	7	Achene	Barochory	-	-	-	3	2	2	-	-	-
Rubiaceae	<i>Galium normanii</i> Dahlj. ^{c,d}	-	-	-	-	-	-	-	-	-	1	1	1
Typhaceae	<i>Typha latifolia</i> L. ^{a,f}	10	Achene	Anemochory	2	2	1	-	-	-	-	-	-
Total					42	12	17	3851	57	3264	1613	18	365

Note: The Ellenberg F number (Hill et al., 1999), fruit type and dispersal syndrome (Julve, 1998) are shown in bold. UK: native (a), alien (b) and absent (c). Iceland: native (d), alien (e) and absent (f) according to Stace (2019). Not shown are winter samples (January, n = 9), which contained one seed of *Stellaria media* (barochory; F = 5; capsule).

35 species, one is considered a weed, four are alien to either the UK or Iceland, only four have an "endozoochory syndrome", and only eight are aquatic plants (Table 1). Overall, 14% of faecal samples contained at least one intact seed. Five species from three families were successfully germinated from the wetland autumn samples that were processed within 3 months of collection (Table S3).

3.1 | Seasonality

Only six plant species (from 4 families) were recorded in UK spring samples, compared to 23 species (12 families) during autumn in the UK, and 8 species (from 5 families) during autumn in Iceland (Table 1). Two species recorded in spring are absent from Iceland (*Juncus effusus* and *Typha latifolia*). Only one seed was recorded in winter (Table 1). In the UK, the prevalence of seeds was significantly higher during autumn than spring migration (binomial glm, z-ratio = 2.621, $p = 0.024$). Prevalence was also significantly higher in Icelandic than in UK samples (autumn: z-ratio = 3.339, $p = 0.0024$; spring: z-ratio = 4.398, $p < 0.0001$). In spring, only 6% (95% CIs = 0.0283, 0.0923) of samples contained at least one seed, compared to 15% of autumn samples from the UK (CIs = 0.114, 0.185) and 72% from Iceland (CIs = 0.508, 0.932).

The total number of seeds per sample (including zeros) differed between UK migration periods, with significantly more seeds in autumn than in spring (t-ratio = 5.078, $p < 0.0001$). UK spring samples also had fewer seeds than Icelandic autumn samples (t-ratio = 3.581, $p = 0.0011$), but differences between autumn samples from the UK and Iceland were not significant (t-ratio = 1.1790, $p = 0.1739$). For samples with seeds, we found no significant differences between seasons or countries in the number of plant species per sample. However, rarefaction analysis showed that there was lower species richness in spring for a given sampling effort (Figure S5). Furthermore, autumn species richness for 25 samples was higher in Iceland than in the UK (Figure S5).

There were significant differences in the composition of plant communities recorded in faecal samples between the UK spring, UK autumn and Iceland autumn periods ($p = 0.001$, Figure S1). Pairwise comparisons showed that all three migration categories were significantly different from each other ($p = 0.001$, Figure S1). Resampling showed these differences were mainly caused by *Vaccinium myrtillus* (dev = 25.3, $p = 0.001$) characteristic of autumn in Iceland, *Poa annua* (dev = 16.2, $p = 0.002$) and *Juncus bufonius* (dev = 11.6, $p = 0.018$) characteristic of autumn in the UK, *Empetrum nigrum* (dev = 21.3, $p = 0.001$) characteristic of autumn dispersal in general, and *Juncus gerardii* (dev = 16.2, $p = 0.002$) characteristic of UK spring dispersal (Table 1).

The relative frequency of five dispersal syndromes among the seeds recorded varied with both season and latitude. In spring, the epizoochory syndrome was dominant in numbers of both species and seeds, and the endozoochory syndrome was absent (Figure 1). In autumn in the UK, the epizoochory syndrome was less dominant, and the endozoochory syndrome was recorded at low frequency. In contrast, in the autumn in Iceland the endozoochory syndrome was dominant in numbers of both species and seeds (Figure 1).

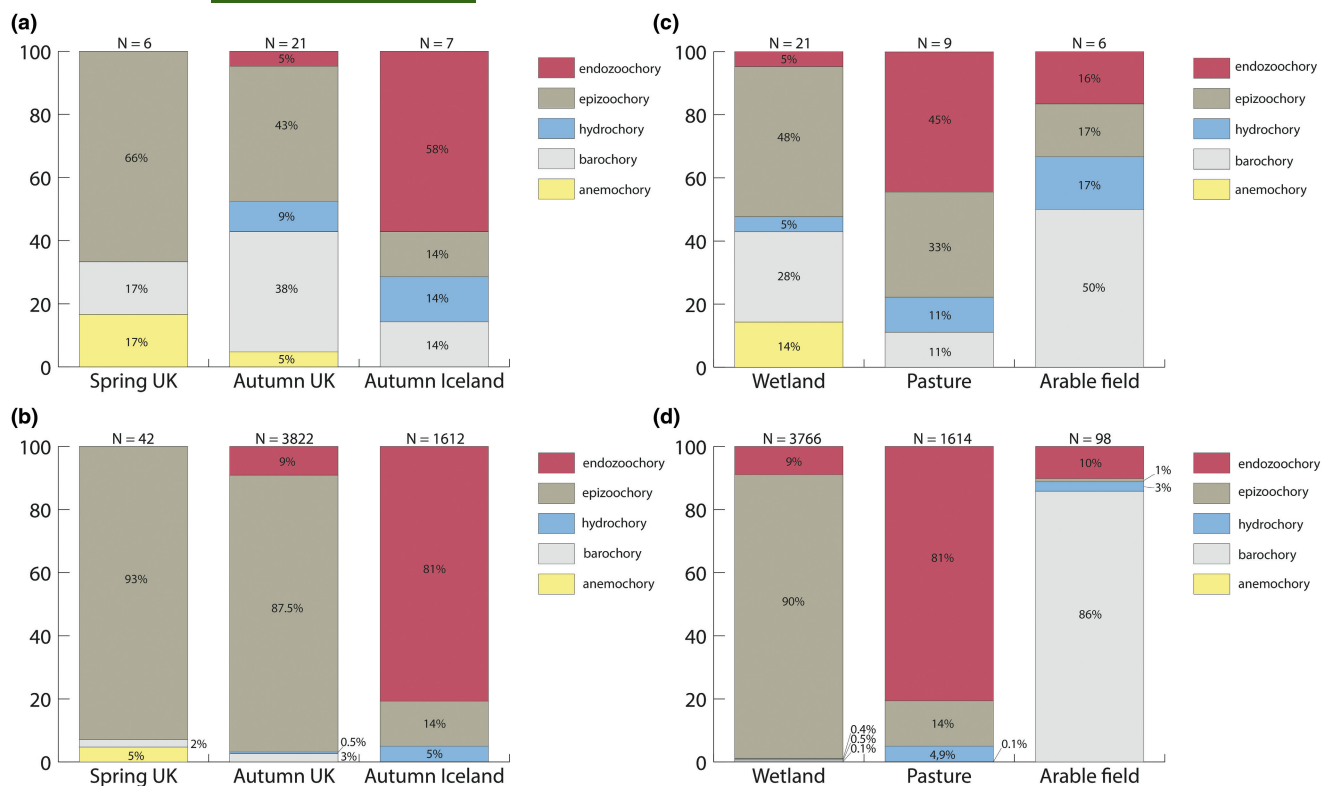


FIGURE 1 Proportions of (a) plant species (N =number of species) and (b) plant diaspores (N =number of intact diaspores) recorded in faecal samples during different migratory periods, according to dispersal syndromes. Proportions of (c) plant species (N =number of species) and (d) plant diaspores (N =number of intact diaspores) recorded in faecal samples in different habitat types (combining pasture in UK and Iceland), according to dispersal syndromes.

Overall, seeds were recorded from plants with Ellenberg F values ranging from 4 to 10 (Figure S2). Aquatic seeds were dominant in the Autumn UK samples, and terrestrial seeds in other samples. During spring migration, only one aquatic species was recorded (*Typha latifolia*, Figure S2 and Table 1).

3.2 | Habitat types

We compared 195 samples from wetlands, 179 from pasture, and 240 samples from arable habitats, and found the greatest prevalence and species richness of seeds in wetlands. Wetland samples contained 21 species (from 11 plant families), compared with 10 species (7 families) in pasture, and 7 species (6 families) from arable habitat (Table S3). In wetlands, 27% (CIs=0.153, 0.267) of samples contained at least one seed, compared to 15% (CIs=0.103, 0.210) in pasture and 7% (CIs=0.038, 0.103) in arable. Seed prevalence was significantly higher in wetlands than in arable (z -ratio=-4.151, p =0.0001). For samples with seeds, wetlands had significantly more seeds per sample than arable habitat (t -ratio=-8.317, p <0.0001). The number of species per sample were not significantly different between habitat types.

The plant communities recorded in different habitats were significantly different (manyglm analysis, p =0.001, Figure S1). Pairwise comparison showed that each habitat is different from the others (p <0.001). Resampling showed the following species

contributed significantly to these differences (Table S3): *Empetrum nigrum* (dev =23.5, p =0.001) and *Poa annua* (dev =16.1, p =0.002) were characteristic of pasture, whereas *Juncus gerardi* (dev =15.6, p =0.002), *J. bufonius* (dev =11.1, p =0.011), and *J. acutiflorus* (dev =8.9, p =0.046) were characteristic of wetlands.

The relative frequencies of dispersal syndromes varied between habitats, especially in terms of seed abundance (Figure 1). Seeds from the epizoochory syndrome were dominant in wetlands, from the endozoochory syndrome in pasture (largely owing to Icelandic samples), and barochory (i.e. unassisted dispersal) in arable fields (Figure 1).

There were differences in moisture requirements between habitats, and seeds of aquatic plants were only dominant in wetland habitats, whereas dry soil plants of Ellenberg $F \leq 5$ were dominant in arable fields. The modal F value was five in arable, six in pasture and nine in wetlands. However, there was much overlap consistent with dispersal of seeds between habitats (Figure S2 and Table S3).

3.3 | Movements and likely LDD events

3.3.1 | Spring migration

There were 10 UK sampling areas in spring for which tracked geese were present within 15 calendar days of faecal sampling (Table S2). After leaving these sampling areas, the mean time these geese took

to reach Iceland was 27.5 h (range 10–92 h). Movements away from faecal sampling areas suggest that seeds retained for up to 24 h can be dispersed >1600 km directly to Iceland, or over several hundred km from north-west England to north-east Scotland (Figure 2a). Geese departing from English sampling sites usually moved towards northern parts of Scotland for a stopover of several days, often at our Scottish sampling sites (e.g. Loch Leven), before making a non-stop flight to Iceland (Figure 2a). There were four birds that reached Iceland from Scotland within 24 h of departure from the sampling areas (Figure 2a). Maximum arrival distances to sampling areas ranged from 131 to 308 km, while maximum departure distances from the sampling points ranged from 65 to 2003 km (Table S2). Between arrival at, and departure from, sampling areas, geese regularly made daily movements of 12–21 km likely to provide seed dispersal over these distances (Figure S3).

3.3.2 | Autumn migration

During autumn migration, many trajectories arrived directly to our UK sampling areas from Iceland (Figure 2b), suggesting that seeds

retained within geese for up to 24 h can be readily dispersed southwards to the UK. The mean time taken to reach one of our UK sampling areas by geese leaving Iceland was 31 h (range 12–318 h). Some tagged individuals arrived in northern Scotland and then headed south some days later, while other individuals headed directly south towards sampling locations close to the English border (Cowcourse and Barrasgate) and remained there for some days (Figure 2b and Figure S4a). The majority of the trajectories and daily movements were related to sampling areas in north-west England that held major roosts (Figure S4b). Six tagged individuals departed from these sampling areas to eastern England. Importantly, some individuals also made extensive movements northwards between areas within the UK of up to 400 km (e.g. from Barrasgate to the Hebrides; Figure 2b), suggesting that northwards seed LDD can occur in autumn, as well as during spring migration.

The locality we sampled in Iceland in autumn had only one tracked bird within 20 km (Figure 2b). However, within 15 days of the sampling date there, a total of 12 tagged birds departed from Iceland and reached several of our UK sampling sites within 24 h (Figure 2b). Maximum arrival distances to our autumn sampling areas ranged from 137 to 2225 km, while maximum departure

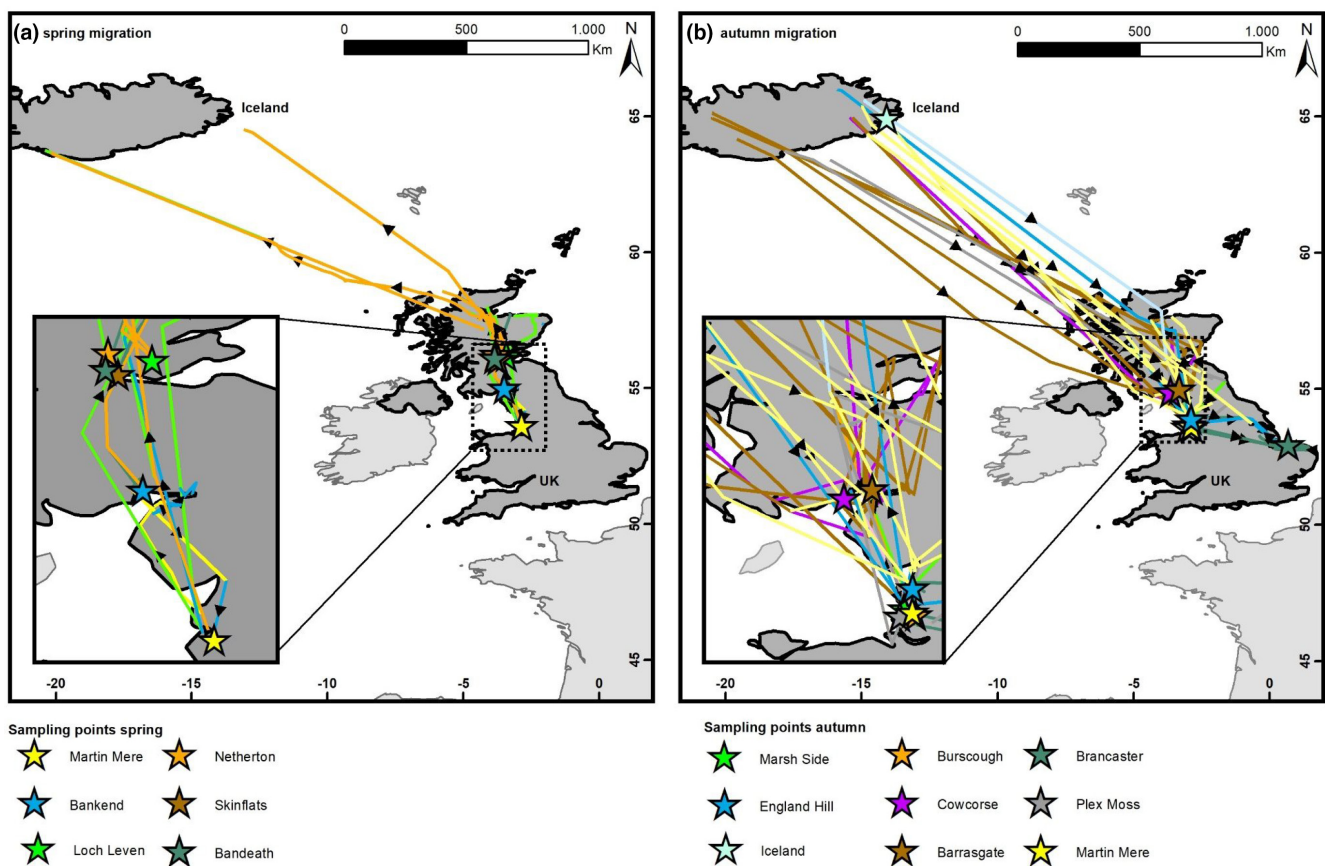


FIGURE 2 Location of faecal sampling areas during migration in the UK and Iceland, and trajectories of tracked Pink-footed geese (including close-up of UK trajectories) (a) during spring migration in 2018 (a); and during autumn migration in 2016–2018 (b). Maps with WGS 1984 projection. Coloured trajectories show movements during up to 24 h before the arrival at, and after departure from, sampling areas (represented by coloured stars) by tracked individuals within a time range of ± 15 days from the sampling date (see Table S2). Some individuals overlap in trajectories, as their trajectories involved more than one sampling area. Intermediate daily movements made between arrival and departure were excluded (but see Figure S3 for spring migration and Figure S4 for autumn migration).

distances from the UK sampling areas ranged from 111 to 255 km (Table S2). In the Iceland sampling area, there was a much greater departure distance of 1337 km (Table S2). In between arrival at, and departure from, sampling areas, geese based there often made daily movements likely to disperse seeds over distances of ≥ 19 km (Figure S4).

4 | DISCUSSION

We combined empirical data on dispersed seeds and goose movements to demonstrate the capacity of pink-footed geese (PFG) to carry out long-distance dispersal (LDD) of different terrestrial and aquatic plants via endozoochory, along the flyway between England, Scotland and Iceland. We found that several different habitats act as propagule sources for endozoochorous dispersal, with major spatial and temporal differences in the dispersed plant communities.

Our study extends existing knowledge of seed dispersal by migratory geese (see review by Green et al., 2016). In arctic Greenland, the migratory Canada goose (*Branta canadensis*) and barnacle goose (*B. leucopsis*) are important plant dispersers (Bruun et al., 2008; Green et al., 2018). In central Europe, endozoochory has been documented for lesser-white fronted geese (*Anser erythropus*) and the widespread greylag goose (*A. anser*; Tóth et al., 2016). Greylags were found to disperse at least 22% of the vascular plants in Baltic archipelagos (Hattermann et al., 2019). Moreover, in southern Europe the greylag goose disperses rare plants such as *Elatine gussonei* (Takács et al., 2017).

It has previously been speculated that the potential for LDD during migration might be low because geese may empty their guts before long-distance flights (Clausen et al., 2002). However, we are unaware of any evidence for this, and similar speculation has been rebutted in the case of shorebirds carrying seeds and migrating from the UK to Iceland, which also do not empty their guts beforehand (Lovas-Kiss et al., 2019). Forced activity in mallards (*Anas platyrhynchos*) had little effect on gut retention time of seeds, but increased the proportion of ingested seeds which survived gut passage (Kleyheeg et al., 2015). Furthermore, gut retention time is generally much longer for herbivores such as geese than for true frugivores (Yoshikawa et al., 2019). In addition, there is no known mechanism for birds to completely clean their guts of seeds and other contents, and birds carry seeds during migratory flights (Viana et al., 2016). Existing experiments on geese retention times (García-Álvarez et al., 2015; Reynolds & Cumming, 2016) provide a valid basis for predicting seed dispersal distances during migration.

Our germination results confirm that seeds survive the digestive tract of PFG, and the low germination is explained by the delay in separating seeds from our samples. When seeds are separated quickly from goose faeces, germination is much higher (García-Álvarez et al., 2015; Reynolds & Cumming, 2016), as also recorded for ducks and other waterbirds (Martín-Vélez et al., 2021; Uryán et al., 2023). Furthermore, seeds which do not germinate during trials are often dormant and still viable (Green et al., 2018).

4.1 | Dispersal syndromes do not predict long-distance dispersal

We found PFGs to disperse 35 terrestrial and aquatic plant species by endozoochory during migratory periods, 31 of which lack an “endozoochory syndrome” (which would be more appropriately considered as the “frugivory syndrome”) and nine of which have a barochory (gravity) syndrome. Given the great abundance and wide distribution of migrating PFGs, they will disperse many more plant species, as demonstrated for other waterfowl that have been studied more intensively (Almeida et al., 2022; Soons et al., 2016). Our results are further supported by Welch (1993) who germinated seeds of *Juncus bufonius*, *Sagina procumbens*, *Taraxacum maculosum* and other unidentified plants from droppings of PFG recovered as soon as they landed in Scotland from Iceland. It is also considered likely that *Ranunculus reptans* is repeatedly brought by PFG from Iceland to the UK by endozoochory (Chater & Rich, 1995). It is noteworthy that *J. bufonius* is the only one of these four species recorded in our study, further suggesting that many additional plant taxa undergo LDD by PFG.

Our results demonstrate clearly how morphological dispersal syndromes should not be used to make predictions about maximum dispersal distances, or LDD mechanisms. Rather than relying on syndromes to make predictions about zoochory for angiosperms which lack a fleshy-fruit, more empirical studies are needed to understand the role of migratory birds and other animals in seed dispersal, and other traits (e.g. seed size, shape and hardness) may be more helpful to make predictions than syndromes (Almeida et al., 2022; Green et al., 2022, 2023).

4.2 | Differences observed between the UK and Iceland in plants dispersed

We recorded seeds of 19 plants found both in the UK and Iceland, suggesting that PFGs could be important vectors for gene flow between these populations. We recorded seeds of 10 plants in the UK that are currently absent from Iceland, which might be expected to become established in Iceland as soon as conditions there become warm enough through climate change. This includes *Juncus effusus* and *Typha latifolia*, whose seeds we recorded during spring, northward, migration. Our results support previous genetic and floristic analyses that find historical plant dispersal events to Iceland and other North Atlantic islands to be consistent with goose migration routes (Alsos et al., 2015). The abundance of migratory geese breeding in these islands may partly explain why they have experienced a rate of successful plant species colonization that is several orders of magnitude higher than that for oceanic islands that lack migratory waterbird populations, such as the Azores or Hawaii (Alsos et al., 2015).

There is a clear asymmetry in the distributions of plants recorded in PFG faeces from the UK and Iceland, as could be expected from the latitudinal gradients in the diversity of plants dispersed by other waterbirds such as ducks (Brochet et al., 2009)

and grey herons (Navarro-Ramos et al., 2021). Only one species *Galium normanii* is exclusive to Iceland, whereas 10 species are in the UK but not Iceland (Table 1). We found evidence that PFG are more frugivorous in Iceland than in the UK, with a strong latitudinal trend in the importance of the endozoochory syndrome among seeds dispersed in autumn. This is consistent with previous literature on PFG diet (Kear, 2005), and latitudinal trends in the distribution of *Empetrum* spp. and *Vaccinium* spp. (Bell & Tallis, 1973; Jacquemart, 1996, 1997; Ritchie, 1955, 1956). Similarly, the endozoochory syndrome is more frequent at extreme latitudes among seeds dispersed by the Canada Goose *B. canadensis* (Green et al., 2018; Neff & Baldwin, 2005).

In contrast to studies of waterbirds in ricefields (Martín-Vélez et al., 2021), we found little evidence that PFG disperse weeds and problematic alien plants associated with agricultural habitats. Four species dispersed by PFG are considered native in the UK but alien in Iceland (Table 1). Our results beg the question as to whether these may partly be species that have colonized via natural vectors such as PFG, after conditions have become suitable via climate change or changes in land-use (i.e. neonative species sensu Essl et al., 2019). Our study suggests seeds of these species are likely to be reaching Iceland via PFG, although human vectors are more likely to explain existing botanical records of these species from Iceland (P. Wasowicz, pers. comm.).

4.3 | Goose movements

Given the great mobility of PFG and their migration patterns, they could disperse plants polewards at a rate exceeding the 100km a decade that may be required to track the impact of global heating on climatic conditions $>60^\circ$ from the equator (González-Varo et al., 2021). Tagged birds migrating from Iceland in the autumn arrived directly to all the wintering regions in the UK (with $>80\%$ arriving to Scotland), and birds returning in spring leave directly from all regions apart from eastern England (Wood et al., 2020). It is noteworthy that several tagged geese reached Iceland within 24h from our sampling areas, despite the fact that we did not sample in the northernmost areas of Scotland used as a last stopover by most PFG. There are also other major roosts further north in Scotland (Wood et al., 2020) which we did not visit, and are likely to be particularly important for seed LDD to Iceland.

Pink-footed geese also likely readily disperse seeds over distances of 100–500km as they move between different regions within the UK (Figures 2), even during the non-breeding period (Wood et al., 2020). We found that daily movements in and around each faecal sampling area can disperse seeds >10 km (Figures S2 and S3) and provide what can be considered as LDD, since even 5 km is much farther than is typically considered LDD for avian frugivores, and much farther than the maximum dispersal distances generally reported for seeds by wind or water (Bullock et al., 2017). A more detailed analysis of daily feeding flights across the UK by 73 tagged PFG found that 62% of feeding locations were within 5 km of the

roost, and 15% were >10 km from the roost, with a maximum of 90 km (Wood et al., 2020).

4.4 | Endozoochory between habitats

Previously, spatial differences in the species composition of seeds dispersed by endozoochory were demonstrated for mallards in Hungary (Lovas-Kiss et al., 2018). We found clear differences among different habitat types in the plant species and communities represented in goose faeces, as expected if seeds are ingested within the habitats where they were egested. However, given the high mobility of the PFG, it is inevitable that many seeds are moved between different habitats used for feeding and roosting. The time interval between movements between habitats (e.g. from a wetland roost to an agricultural field) is often much shorter than gut seed retention time (García-Álvarez et al., 2015; Reynolds & Cumming, 2016), so faeces also contained seeds from species associated with different habitats. Likewise, we recovered many seeds from aquatic species from a grassland in Iceland, suggesting these seeds were ingested in nearby wetlands. Many of the crowberry (*Empetrum nigrum*) seeds we recorded in north-west England were recovered from faeces from a newly arrived flock in an area where this plant species is not recorded, suggesting these geese had ingested berries in Scotland or Iceland.

4.5 | Seasonality

There were strong seasonal effects in the rates of seed dispersal and in the communities dispersed by PFG. Those plants dispersed during spring migration, and which may therefore readily keep pace with climate change, were almost exclusively terrestrial plants lacking a fleshy-fruit. The six plant species found in the spring samples are summer bloomers, beginning to produce flowers in the early spring and remaining in flower until early September (Fitter & Peat, 1994). Hence, for spring seed dispersal, the geese probably ingested seeds still remaining on the parent plant from the previous year, or took them from the water surface or from the seed bank in soil or sediments while feeding or drinking. This suggests that, while the phenology of fruiting limits the potential of fleshy-fruited plants to be dispersed towards cooler latitudes (as shown for frugivorous passerines by González-Varo et al., 2021), this is not the case for other terrestrial plants. Our results are consistent with those of Uryán et al. (2023), who found that a variety of terrestrial plants lacking a fleshy-fruit are dispersed by Hungarian mallards during spring migration, whereas more dispersal of aquatic plants occurs during autumn migration. Although we found that fewer seeds are carried by geese during spring than autumn migration (as previously recorded for Icelandic black-tailed godwits (*Limosa limosa islandica*) by Lovas-Kiss et al., 2019), even rare seed LDD events have major implications for plant distributions and genetic exchange (Nathan et al., 2008).

5 | CONCLUSIONS

Under ongoing climate change, rapid redistribution of plant species is vital to maintain the functioning of terrestrial ecosystems, yet we remain ignorant of LDD processes. More research is needed into the role that migratory geese and other waterfowl play in moving seeds between land masses, and in allowing different plants to keep pace with climate change. Until now, climate change may have benefitted the PFG and other waterbirds breeding at higher latitudes (Amano et al., 2020). However, that is set to change, and global heating is forecast to reduce the PFG breeding range by 59% over the next three decades (Nagy et al., 2021). Our study emphasizes the need to conserve populations of PFG and other migratory waterbirds breeding at extreme latitudes, to ensure the maintenance of seed dispersal services.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The dataset of the dispersed species and the telemetry data required to our analysis is available at <https://doi.org/10.6084/m9.figshare.22717603>.

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BIOSKETCH

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Victor Martin-Velez is interested in waterbird movement ecology, and its applications to understand the ecosystem services of waterbirds. Specifically, the role of waterbirds in biovectoring seeds, pollutants and diseases (including antibiotic resistances). Other interests are related with network analyses, GIS and Spatial Ecology.

Kane Brides main areas of interest are in population dynamics, ecology & movements of waterbird species globally. Further work areas include leading on bird ringing, GPS tagging & census based surveys.

Dave Wilkinson has wide interests in ecology and the environmental sciences. His interests in birds, seed dispersal and the problems with conventional classifications of 'animal dispersed' go back to a paper he published in this journal in 1997.

Larry Griffin is now a consultant zoologist/botanist after 25 years of researching wildfowl including scoters, geese and swans in particular. He is particularly interested in the welfare-friendly tracking of wildfowl to establish ontogeny of migration, responses to climate change in the High Arctic and individual and cultural responses to such changes, and the value of species as ecosystem engineers.

Andy J. Green is mainly interested in wetland and waterbird ecology, particularly the role of waterbirds as dispersal vectors for all kinds of organisms, as well as plastics and other contaminants. Other interests include biological invasions, restoration ecology and conservation genetics.

Author Contributions: ÁL-K, DMW and AJG conceived the ideas and designed methodology; AJG, ÁL-K, KB, DMW and LRG collected the data; ÁL-K and VMV analysed the data; ÁL-K and AJG and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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