RESEARCH ARTICLE

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Plants dispersed by a non-frugivorous migrant change throughout the annual cycle

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Abstract

Aim: Migratory waterfowl are important endozoochory vectors for a range of plants lacking fleshy fruits. Our aim was to study the critical question of how endozoochory rates change throughout the annual cycle, and how this relates to plant life-form and phenology.

Location: Lake Velence, Hungary.

Time period: 2017–2018.

Major taxa studied: Mallard (*Anas platyrhynchos*), Angiospermae, Charophyta.

Methods: We studied waterfowl endozoochory, quantifying seeds and other diaspores dispersed by mallards by collecting faecal samples monthly ($n_{total} = 670$) at a Hungarian lake. We tested the germinability of all seeds recovered from the faecal samples.

Main conclusions: We extracted 5,760 seeds representing 35 plant taxa from mallard faecal samples, and 40% of these seeds germinated successfully following gut passage. We found major differences between seasons in the species composition of the seeds recovered. The peak in species diversity and in abundance of terrestrial seeds coincided with the spring migration of mallards. Importantly, endozoochory was only strongly synchronized with seed production in submerged, but not in emergent or terrestrial plants, illustrating the potential for endozoochory of seeds ingested from the soil seed bank. Overall, our results suggest that endozoochory by migratory waterfowl is a strong and underestimated driver of plant distributions, and is likely to facilitate plant range shifts under climate change, and after introduction of alien species.

KEYWORDS
dispersal, phenology, seasonality, seed bank, waterfowl, wetland

1 | INTRODUCTION

During dispersal, organisms move from their place of birth and/or reproduction to a new location (Tesson et al., 2015). Each species has its own preferred climatic conditions, and these 'climatic envelopes' are shifting towards the poles and higher altitudes due to climate change, increasing the need for dispersal (Lenoir et al., 2020; Lenoir & Svenning, 2015). In the case of plant species, there is limited information on their dispersal mechanisms and potential for climate change-induced range shifts (Corlett & Westcott, 2013; González-Varo et al., 2017; Lenoir et al., 2020; Lenoir & Svenning, 2015; Urban et al., 2016). To keep pace with climate change, long distance

dispersal is vital, and can potentially be provided by migratory birds that carry seeds (Green et al., 2022; Viana, 2017). Dispersal interactions between frugivorous birds and plants are considered key to the stability and persistence of both bird and plant communities (Carlo et al., 2003; Kitamura et al., 2002; Moran et al., 2004). However, fleshy-fruited plants have limited capacity to keep pace with climate change because their fruits are rarely available to frugivorous birds during spring migration (González-Varo et al., 2021). Much less research has focused on the role of non-frugivorous waterbirds in plant dispersal, yet there is increasing evidence that they disperse a broad range of plants by endozoochory (i.e., transportation through the digestive tract) because an important fraction of seeds survive gut passage, while digestion can also help to break seed dormancy (Green et al., 2022; Soons et al., 2016). Migratory dabbling ducks alone (including mallards *Anas platyrhynchos*) are known to disperse over 400 angiosperms in Europe, including a broad range of terrestrial and aquatic species (Soons et al., 2016), but the true number may be much higher (Lovas-Kiss, Vizi, et al., 2018). The great majority of these plants are among the 92% of European species that lack a fleshy fruit (Green et al., 2022). Moreover, alien and weed species can be dispersed in abundance by waterbirds (Green, 2016; Lovas-Kiss et al., 2019; Lovas-Kiss, Sánchez, et al., 2018; Martín-Vélez, Lovas-Kiss, et al., 2021). Traditional dispersal syndromes have not helped to predict which plants are dispersed by waterbirds, or whether they are dispersed by endozoochory or epizoochory (i.e., transportation on the plumage or on the feet, Coughlan et al., 2017). A large fraction of plants dispersed by endozoochory are currently assigned to 'unassisted' or other abiotic syndromes (Green et al., 2022; Lovas-Kiss, Vizi, et al., 2018). This underlines the need for more research into waterbird endozoochory.

While spring migration of birds potentially plays a crucial role in dispersing plants in the face of climate change, seed production generally overlaps more with autumn migration. If waterfowl only ingested diaspores (seeds from hereon) when they are produced, or took them from the parent plant, they would be unlikely to disperse them during their spring migration (Clausen et al., 2002). However, waterfowl often ingest seeds from soil seed banks, and endozoochory has been recorded in all seasons (Brochet, Guillemain, Fritz, et al., 2010; Green et al., 2016). Nevertheless, as yet there are no detailed studies of how plant phenology relates to waterfowl endozoochory, or how endozoochory rates change seasonally. Different patterns might be expected for aquatic plants (whose seeds are released in habitats frequented by waterbirds) and terrestrial plants (whose seeds may be blown or washed into water before ingestion by waterfowl).

We present a year-round study with monthly sampling of endozoochory by mallards at a single lake. The mallard is the most widespread waterfowl species in Europe and provides a proxy for dispersal carried out by other waterfowl species (Sebastián-González et al., 2020). Spatial models have confirmed their endozoochory potential during both long-distance migrations and daily movements between different wetlands (Kleyheeg et al., 2019; Kleyheeg, Treep, et al., 2017; Viana et al., 2013).

We investigated seasonal differences in the abundance and composition of plant seeds dispersed by mallards, and related them to the habitat and phenology of the plant species recorded. We collected faecal samples monthly, and quantified the seeds of aquatic and terrestrial plants present, as well as their germinability, morphological dispersal syndrome and whether they are weeds and/or alien species. Our working hypotheses were as follows: (a) Plants dispersed by mallards would be mainly those classified into abiotic dispersal syndromes in plant databases (after Green et al., 2022). Terrestrial plants would be mainly weeds and alien species, due to the urban habitats surrounding the lake where samples were collected. (b) The species composition of seeds dispersed would vary seasonally, especially owing to variation in the phenology of seed production. Hence, dispersal rates would be much higher in autumn than in spring. Variation between samples in species composition (β-diversity) would be greatest in seasons with more terrestrial plants, because numerous terrestrial species are dispersed, but each of them in low abundance (Soons et al., 2016). (c) Seeds of aquatic plants would generally be more abundant, but the proportion of aquatic plants would be relatively higher in months when these seeds are produced, since terrestrial seeds are more likely to be taken from the seed bank, chiefly at times when aquatic seeds are not available (Thompson & McCarthy, 2008). The relative abundance of weeds would mirror that of terrestrial plants, since few weeds are aquatic.

2 | METHODS

2.1 | Study animal

The mallard (*A. platyrhynchos*) is a generalist, omnivorous species that occurs in all wetland habitats (e.g., marshes, lakes, artificial ponds, reservoirs, rivers) in Europe (Cramp et al., 1977; Dessborn et al., 2011). Hungary holds a mixture of a resident minority that move within Hungary and spend the winter in unfrozen waters, and a migrant majority (Supporting Information Figure S3). In autumn, large numbers of wintering birds arrive that breed across north and north-east Europe (Figure 1, see also Liker & Nagy, 2009). The maximum recovery distance for a ringed bird was 2,304 km (from Russia). Migrants that breed in Hungary winter across the Mediterranean and Black Sea regions (Csörgő et al., 2009, Figure 1).

2.2 | Study site

Lake Velence is a 24-km^2 permanent soda lake, the third largest natural lake in Hungary (Reskóné, 1999). It has an average depth of 1.5 m; water levels are relatively stable due to connections with two reservoirs (Báldi & Kisbenedek, 2000; Borics et al., 2016). The maximum extent of water level fluctuation is 30 cm, and maximum depth is reached between March and May. Lake Velence is a Natura 2000 site and an Important Bird Area (Wetland International, 2020). Despite its brackish character, freshwater marsh vegetation is found
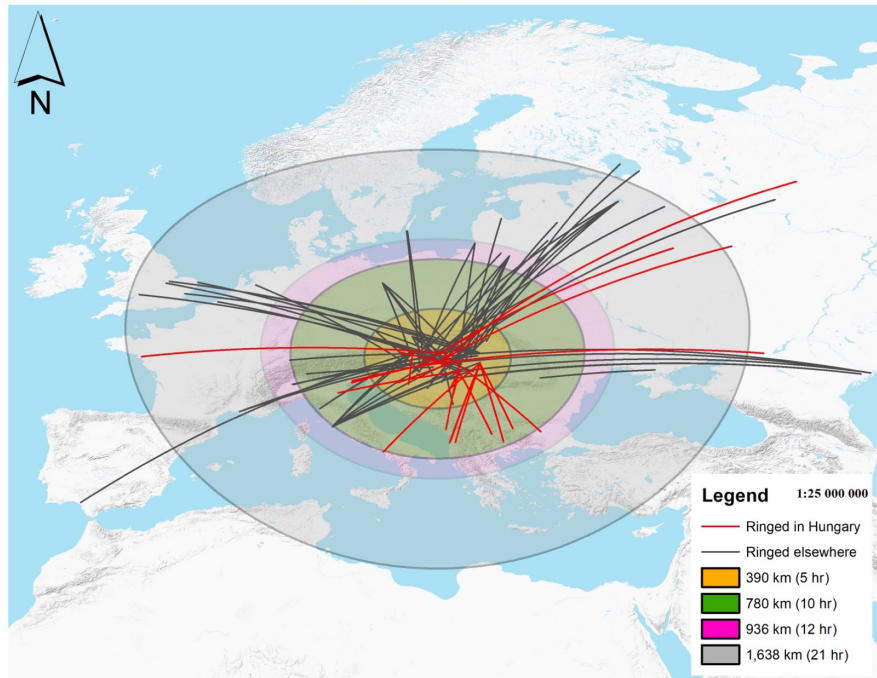
FIGURE 1 Migratory movements of mallard individuals ringed or recovered (captured or shot) within the historical borders (before WW1) of Hungary. Each line represents a recovered mallard individual. Ringing data were acquired from BirdLife Hungary. Birds both ringed and recovered in Hungary are excluded. Circles represent potential dispersal distances during migration, calculated according to the method described in Farmer et al. (2017) using experimental retention times for germinated seeds (Agami & Waisel, 1986; Figuerola et al., 2010; Lovas-Kiss et al., 2020; Soons et al., 2008). Retention times ≥ 21 hr with viable seeds have been recorded, for example, for *Chenopodium album*, *Echinochloa cruss-galli*, *Bolboschoenus maritimus*, *Schoenoplectus litoralis*. Shorter retention time intervals with viable seeds shown are reported in the same papers, with maxima of 12 hr (e.g., Najas marina), 10 hr (e.g., *Lycopus europaeus*) and 5 hr (e.g., *Phragmites australis*, *Sparganium erectum*)

in the western part of the lake (Besnyői & Illyés, 2010). A variety of other water bodies are found within 20 km (Supporting Information Figure S2), and are likely inter-connected by daily mallard movements (Kleyheeg, van Dijk, et al., 2017). Over the study year, the number of mallards in Lake Velence varied between a peak of 2,648 individuals in November and a minimum of 95 in April (Faragó, 2021).

2.3 | Sample processing

From September 2017 to August 2018, fresh mallard faecal samples were collected in the middle of each month from four sites situated on the lake's shore, including boat moorings and paved shorelines (Supporting Information Figure S2). After locating monospecific flocks, we flushed resting birds to collect their fresh droppings. The distance between samples exceeded 1 m to avoiding multiple sampling of the same individual. We immediately removed any plant parts or soil attached to the dropping and visible to the naked eye, then stored samples in sealable plastic bags placed in a refrigerator at +4 °C until processing. Birds at these sites were occasionally fed by tourists, mostly with bread. In some months, the birds were absent at some sampling sites, owing to their constant movements; therefore not all sites were sampled in each month. Over 12 months, we collected a total of 670 samples (19–101 per month, Urgyán et al., 2022).

During laboratory processing, first, any external contaminants (fruits, seeds or other tissues that were attached to the dropping) not visible to the naked eye were removed under a stereomicroscope. All the samples were weighed using an Ohaus EP213C Explorer® Pro scale. Each sample was then washed with distilled water in a 100-μm sieve, before sorting and counting undamaged plant diaspores under a stereomicroscope, taking photographs to aid identification. All these diaspores were identified, based on their colour, shape, pattern and size, using the 'Digital seed atlas of Netherlands' (Cappers et al., 2012) and 'Atlas of seeds and fruits of Central and East-European flora' (Bojnanský & Fargašová, 2007).

Next, seeds were stored dry in Eppendorf tubes until germination trials began. Germination trials were carried out in Petri dishes on 1% nutrient-free agar for terrestrial species, and in cell culture plates filled with distilled water for aquatic species. They were kept at 24 °C during 12 hr of illumination, and at 18 °C in the dark. Seeds were checked daily for germination for 1 month, while we replenished distilled water whenever necessary.

2.4 | Plant categorization and their phenology

For each plant species recorded among the seeds in mallard samples, we extracted the flowering months from the New Hungarian Herbal

(Király, 2009), and calculated the median flowering date as Julian dates. We then calculated the number of days elapsed between median flowering day and the date of sample collection for each sample containing the nominate species. Values range from 0 (i.e., faecal sample containing the seed was collected on the median flowering date of the plant) to 364 (i.e., sample containing the seed was collected 1 day prior to the median flowering date of the species).

In order to categorize the dispersed plant species as weeds and non-weeds, we collected social behaviour types (Borhidi's SBTs, equivalent to Grime's Competitor Stress-tolerator Ruderal strategies, but adapted to the Hungarian flora). We categorized species as weeds if they belonged to the SBT category of plants from anthropogenically disturbed habitats. These are disturbance-tolerant plants, native weed species, alien species (extirpated crop plants; introduced weeds), and secondary habitat competitors (ruderal competitors of native flora). Moreover, we collected the soil moisture requirements (WB, a Borhidi W indicator value based on Ellenberg F values but adapted to the Hungarian flora) to classify the dispersed plants into aquatic and terrestrial species. Species with WB values of 8 or more were characterized as aquatic plants. We subdivided the aquatic plants into emergent (species with an emerged stem above the water surface) and submerged (species living under water and at the water surface) categories. Both WB and SBT values were collected from the Flora database (Horváth et al., 1995). To consider how mallard endozoochory was related to morphological dispersal syndromes, we extracted syndromes for each species from the Baseflor (Julve, 1998) database.

2.5 | Seasonal variation in seed abundance, species richness and species composition

We compared species richness (i.e., total number of plant species represented among the seeds in a single sample) and seed abundance (i.e., total number of seeds found in a single sample) per sample between seasons using a negative binomial generalized linear model with a single predictor (season) and the function *glm.nb* ('MASS' package, Venables & Ripley, 2002), and used the *lsmeans* function (Lenth, 2016) to explore pairwise differences.

To analyse seasonal differences in the plants dispersed by endozoochory, we assigned the months of December, January and February to winter; March, April and May to spring; June, July and August to summer; and September, October and November to autumn seasons. Statistical analyses were performed using R statistical software (version 4.1.2, R Core Team, 2021), especially the 'vegan' package. In order to establish differences in seed species composition among seasons, we used a nonparametric ANOVA (PERMANOVA, Anderson, 2001) test. The significance level for the difference between seasons was determined by random permutation test (with 1,000 replicates), using the *adonis* function. The analysis was based on a matrix of Bray–Curtis differences generated from abundances of the dispersed species with the *vegdist* function and with values ranging from 0 to 1. A Simper post hoc (*simper* function) test was used to identify those plant species whose seeds contributed to significant differences between groups. To illustrate the difference between seasons, we used non-metric multidimensional scaling (NMDS), which was generated using the Bray–Curtis difference matrix and the *metaMDS* function. The heterogeneity of the species composition centroids of the seasons was investigated using the *betadisper* function. This was used to calculate the degree of dispersion of each sample, and the compositional centroid of each season. This procedure is often used to test for β-diversity differences between samples. We used a *TukeyHSD* posthoc test ('stats' package) to determine which seasons differed in β-diversity. For all these analyses, we excluded samples that did not contain any seeds.

2.6 | Coupling between phenology and dispersal

In order to explore how plant phenology is associated with the number of seeds dispersed by mallards (i.e., whether birds were likely to be consuming seeds from the parent plants themselves or soon after their release, or were instead taking them months or years later from the seed bank), we used generalized linear models with Poisson (for submerged and terrestrial species) or quasi-Poisson (for emergent plant species, due to detected overdispersion) error distributions (using R function *glm*). These models contained the number of seeds in a sample as the dependent variable and median flowering date of plant species in the sample (calculated as a weighted average of the median flowering times of the species present in the sample, weighted by the number of seeds belonging to each species, see below) as a single explanatory variable. Median flowering date was tested as both linear and as a second-degree orthogonal polynomial, but the latter was only retained in the final model if the polynomial effect significantly improved model fit. This analysis was performed separately for emergent, terrestrial and submerged plants, only considering seeds belonging to these taxa and only samples containing at least one seed belonging to this category. Overdispersion was checked using the R function *dispersiontest* from package 'AER' (Kleiber & Zeileis, 2008).

2.7 | Aquatic versus terrestrial and weed versus non-weed

We looked at seasonal differences between the proportions of aquatic (both submerged and emergent) and terrestrial plants, as well as weed and non-weed species using binomial generalized mixed models ('stats' package, R Core Team, 2021). In these models we used the proportion of dispersed aquatic to non-aquatic plants (values ranged from 0 = only aquatic taxa to 1 = only terrestrial taxa) or the proportion of weed to non-weed seeds (values ranged from 0 = only weeds to 1 = only non-weeds) as dependent variables and the season of sample collection as a single independent variable. Results of these models were plotted using the 'sunflowerplot' function ('stats' package, R Core Team, 2021). We assessed overdispersion of these models using the function *overdisp_fun* (Bolker, 2018).

3 | RESULTS

During the 12-month study, 670 samples were collected (wet mass 2.69 g ± 0.104; mean ± SE; spring: 176, summer: 163, autumn: 203, winter: 128), containing a total of 5,760 plant diaspores (seeds from hereon) belonging to 35 plant taxa and 15 families. Overall, 42% of samples contained at least one intact seed.

3.1 | Categorization of dispersed plants

Twelve aquatic species were identified, as well as 21 terrestrial species, including four alien terrestrial species (Tables 1 and 2). Moreover, only two species are not recognized as naturalized or alien outside Hungary (Table 2). Two aquatic taxa were not identified to species level (Charophyceae and *Carex* sp.). Among species detected, 19 were classified as weeds, with only two of these being aquatic (Table 2). Only one species was previously listed as having an endozoochory syndrome, compared to seven with an epizoochory syndrome and 25 with abiotic syndromes (Table 1).

Seeds of the emergent *Schoenoplectus litoralis* were dominant (Tables 1 and 2), with 82% of all recovered seeds belonging to this species, which was recorded in all months except October and July. The next most frequently recorded taxon was the submerged macrophyte *Potamogeton pectinatus*, found in eight months, followed by the terrestrial weed *Chenopodium glaucum* found in six months. Most (18) species were only recorded in one month, and nine species were represented by only one propagule. Of all the seeds found, 2,148 germinated in the laboratory (40%), belonging to 13 terrestrial and three aquatic species, representing seven families (Table 2).

3.2 | Seasonal variation in seed abundance, species richness and species composition

Most plant species (25) were found in the samples collected in spring, with significantly more species per sample than in all other seasons [summer (15 species): z-value = −4.953, $p < .0001$; autumn (5): z-value = −2.899, $p = .003$; winter (9): z-value: −2.337, $p = .01$, Supporting Information Table S2]. In contrast, most seeds (2,338) were found in winter, when samples had significantly more seeds per sample (18.3 ± 35.87, mean ± SE) than in spring (5.3 ± 3.31, mean ± SE; z-value: −3.550; $p = .0003$, Supporting Information Table S2) and summer (2.0 ± 3.87, mean ± SE; z-value: −6.058; $p < .0001$). Autumn had significantly more seeds per sample (10.6 ± 27.72, mean ± SE) than summer (2.0 ± 3.87, mean ± SE; z-value: −5.094; $p < .0001$, Supporting Information Table S2).

The PERMANOVA revealed a significant difference between the species composition centres of each season ($df = 3$, $R^2 = .09$, $p = .001$), although the NMDS ordination shows substantial overlap between seasons (Supporting Information Figure S1). Simper post-hoc tests showed that these differences were due to seasonal differences in seed quantities of both aquatic (*Potamogeton*

pectinatus, *Schoenoplectus litoralis*, *Polygonum aviculare*) and terrestrial (*Chenopodium glaucum*, *Chenopodium album*, *Najas marina*) species (see Supporting Information Table S1 for details). β-diversity in species composition between samples differed significantly between seasons ($df = 3$, $F = 11.441$, $p < .0001$). Tukey's honestly significant difference (HSD) test showed a significant difference between spring and autumn months ($p < .0001$), as well as between spring and winter months ($p < .0001$), indicating greater heterogeneity between samples in spring.

3.3 | Coupling between phenology and dispersal

In the case of submerged plants, the abundance of seeds of a given species in faecal samples decreased as more time passed after the median flowering date of that species (z-value = −7.346, $p < .0001$, Supporting Information Table S3, Figures 2 and 3). In contrast, we found significant quadratic relationships in the case of terrestrial and emergent plants, with the highest proportion of seeds recovered from faecal samples that were collected between 150–250 days following the median flowering date of these species (Figures 2 and 3, and Supporting Information Table S3). In both cases, the number of seeds recovered was relatively low both before and after this period.

3.4 | Aquatic versus terrestrial and weed versus non-weed

Significantly more seeds from terrestrial species were found in spring samples compared to aquatic plants (z-value: −6.312, $p < .0001$, Figure 4a). In all other seasons, there were significantly more aquatic than terrestrial seeds (summer: z-value: 12.011, $p < .0001$, autumn: z-value: 18.0403, $p < .0001$ winter: z-value: 28.946, $p < .0001$, Figure 4a, Supporting Information Table S4). Since weed seeds were mainly from terrestrial plants, there were significantly more weeds in spring (z-value: 2.6, $p = .0093$, Figure 4b, Supporting Information Table S4) than in the other seasons.

4 | DISCUSSION

We quantified dispersal of a diverse range of flowering plants throughout the annual cycle by a common waterbird with a world population of around 20 million (Wetlands International, 2022). Throughout the year, mallard endozoochory consistently provided high rates of seed dispersal for plants lacking a fleshy fruit, and previous studies suggest this is likely to be true of other duck species (Soons et al., 2016). The community of plants dispersed, and the relative importance of aquatic and terrestrial seeds, changed seasonally. Waterfowl are shown to be vital seed dispersers for such plants, in a manner comparable to the importance of frugivorous birds as vectors for fleshy-fruited plants (Green et al., 2022), and the mean numbers of seeds we recorded per excreta sample were comparable with those recorded in frugivorous

TABLE 1 The total number of recovered plant propagules from mallard faecal samples (TP), the number of faecal samples containing plant propagules (NS), and the maximum number of propagules in a single faecal sample (MP) for each plant species recovered in each of the four seasons

Plant family	Species	Autumn (n = 203)			Winter (n = 128)			Spring (n = 176)			Summer (n = 163)		
		TP	NS	MP	TP	NS	MP	TP	NS	MP	TP	NS	MP
Amaranthaceae	*Amaranthus blitoides*[a,b,f]							3	1	3			
	Amaranthus retroflexus[a,f]							3	1	3			
	Chenopodium album[f]				2	1	2	65	11	21			
	Chenopodium chenopodioides[b,f]				8	3	6	8	3	5			
	Chenopodium glaucum[c,f]				98	6	41	233	15	170	3	2	2
	Chenopodium polysermum[f]							8	3	5			
Asteraceae	*Conyza canadensis*[a,b,f]							5	2	4			
Caryophyllaceae	*Arenaria serpyllifolia*[b]										1	1	1
Charophyceae	–[e]										22	2	13
Cyperaceae	*Bolboschoenus maritimus*[d]							11	4	8	1	1	1
	Carex otrubae												
	Carex secalina							4	2	3			
	Carex sp.							1	1	1			
	Schoenoplectus lacustris[d,f]	3	2	2				1	1	1			
	Schoenoplectus litoralis[d]	1914	53	330	2213	39	387	324	25	140	245	24	151
Elaeagnaceae	*Elaeagnus angustifolia*[a,f]				2	1	2						
Fabaceae	*Medicago falcata*[b,f]										9	2	6
	Medicago lupulina[c,f]				1	1	1						
	Trifolium pratense[f]							2	1	2	39	1	39
	Trifolium repens[f]				2	1	2	1	1	1			
Haloragaceae	*Myriophyllum spicatum*[e]										2	1	2
Hydrocharitaceae	*Najas marina*[e]	182	13	110							5	4	2
Laminaceae	*Lycopus europaeus*[d,f]							6	3	4			
Plantaginaceae	*Veronica anagallis-aquatica*[d]							1	1	1			
	Plantago major[f]							23	3	21			
	Plantago media[c,f]										1	1	1
Poaceae	*Echinochloa crus-galli*[f]							1	1	1			
	Phleum pratense							55	5	39	1	1	1
	Phragmites australis[d]				1	1	1	18	12	4			
	Poa annua[f]							1	1	1	1	1	1
Polygonaceae	*Polygonum aviculare*[f]	11	7	5				141	24	46	2	2	1
Potamogetonaceae	*Potamogeton pectinatus*[e]	49	21	7	11	4	3	4	2	3	1	1	1
	Potamogeton perfoliatus[e]										1	1	1
Ranunculaceae	*Ranunculus sceleratus*							4	3	2			
Typhaceae	*Sparganium erectum*[d]							1	1	1			
	Total	2,159	96	454	2,338	57	445	924	127	490	334	45	223

[a]Alien species.

[b]Plants not previously detected in the diet of *Anas* species (Almeida et al., 2022).

[c]Species not previously detected in the diet of mallards (Almeida et al., 2022).

[d]Emergent species.

[e]Submerged species.

[f]Weed species.

TABLE 2 Germination characteristics and ecological indicator values of plant species recovered from mallard faecal samples

Plant family	Species	TP	G	GR	DS	WB	Weed	Alien status
Amaranthaceae	*Amaranthus blitoides*[a]	3	2	66.7	Epizoochory	3	Yes	A
	Amaranthus retroflexus[a]	3	0	0.0	Epizoochory	5	Yes	A
	Chenopodium album	67	23	34.3	Barochory	4	Yes	E
	Chenopodium chenopodioides	18	4	22.2	Barochory	6	Yes	E
	Chenopodium glaucum	334	114	34.1	Barochory	6	Yes	E
	Chenopodium polysermum	8	5	62.5	Barochory	6	Yes	E
Asteraceae	*Conyza canadensis*[a]	5	0	0.0	Anemochory	4	Yes	A
Caryophyllaceae	*Arenaria serpyllifolia*	1	0	0.0	Anemochory	3	No	E
Charophyceae	–	22	0	0.0	–	–	–	–
Cyperaceae	*Bolboschoenus maritimus*	12	0	0.0	Anemochory	10	No	E
	Carex otrubae	1	0	0.0	Hydrochory	8	No	N
	Carex secalina	3	0	0.0	Hydrochory	7	No	E
	Carex sp.	1	0	0.0	–	–	–	–
	Schoenoplectus lacustris	4	0	0.0	Hydrochory	12	Yes	E
	Schoenoplectus litoralis	4,696	1,891	40.3	Anemochory	10	No	N
Elaeagnaceae	*Elaeagnus angustifolia*[a]	2	1	50.0	Endozoochory	?	Yes	A
Fabaceae	*Medicago falcata*	9	1	11.1	Epizoochory	3	Yes	E
	Medicago lupulina	1	0	0.0	Barochory	5	Yes	E
	Trifolium pratense	41	23	56.1	Epizoochory	6	Yes	E
	Trifolium repens	3	0	0.0	Epizoochory	5	Yes	E
Haloragaceae	*Myriophyllum spicatum*	2	0	0.0	Hydrochory	12	No	E
Hydrocharitaceae	*Najas marina*	187	0	0.0	Hydrochory	12	No	E
Laminaceae	*Lycopus europaeus*	9	0	0.0	Hydrochory	9	Yes	E
Plantaginaceae	*Veronica anagallis-aquatica*	1	0	0.0	Barochory	9	No	E
	Plantago major	23	1	4.4	Barochory	6	Yes	E
	Plantago media	1	1	100.0	Barochory	5	Yes	E
Poaceae	*Echinochloa crus-galli*	1	0	0.0	Epizoochory	7	Yes	E
	Phleum pratense	56	21	37.5	Epizoochory	5	No	E
	Phragmites australis	19	1	5.3	Anemochory	10	No	E
	Poa annua	2	1	50.0	Barochory	6	Yes	E
Polygonaceae	*Polygonum aviculare*	154	38	24.7	Barochory	4	Yes	E
Potamogetonaceae	*Potamogeton pectinatus*	65	21	32.3	Hydrochory	12	No	E
	Potamogeton perfoliatus	1	0	0.0	Hydrochory	12	No	E
Ranunculaceae	*Ranunculus sceleratus*	4	0	0.0	Hydrochory	9	No	E
Typhaceae	*Sparganium erectum*	1	0	0.0	Hydrochory	10	No	E

Note: TP = the total number of propagules placed to germinate; G = the number of germinated propagules of that species; GR = the % germinability of passed seeds in a given species; DS = dispersal syndrome (following categorization by Julve, 1998); WB = Borhidi's soil moisture requirement indicator values; Weed or not (based on Borhidi's SBTs); alien status: A = alien or naturalized taxon from outside Europe; E = European species that became alien or naturalized outside its native range; N = not listed as alien or naturalized (van Kleunen et al., 2019).
[a]Alien to Hungary.

birds. However, endozoochory in mallards is less coupled with the timing of seed production, and we found they have a higher potential for seed dispersal during spring migration than reported for frugivores (González-Varo et al., 2021). The link between timing of mallard endozoochory and of seed production also varied fundamentally between submerged, emergent and terrestrial plants.

4.1 | Dispersal syndromes and endozoochory of terrestrial plants

The greater number of terrestrial than aquatic plant species found in our study is consistent with the results of a previous meta-analysis on the seeds ingested by mallards and other European dabbling
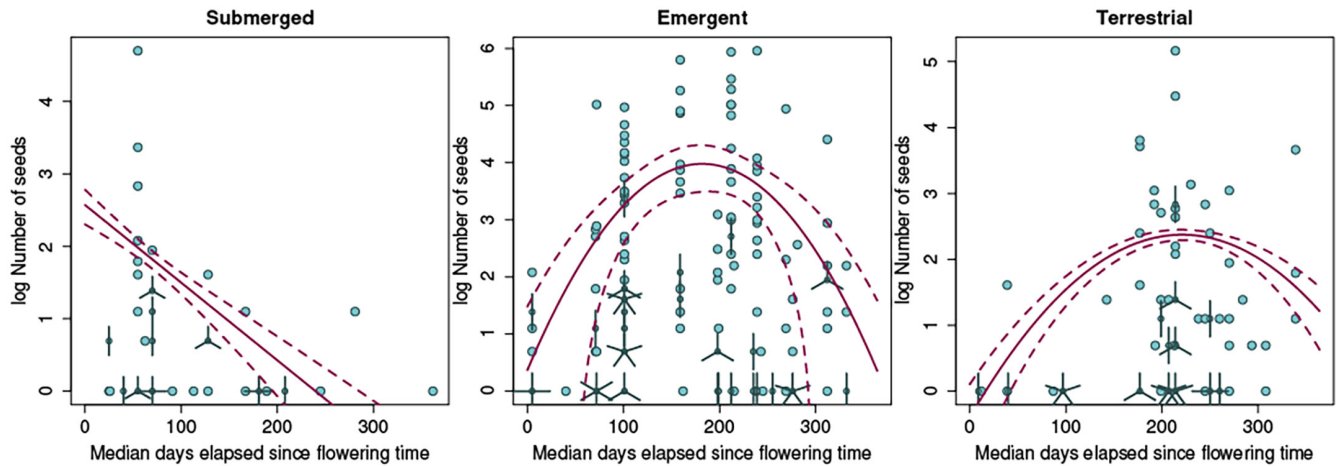
FIGURE 2 Relationship between the abundance of the seeds of submerged, emergent and terrestrial plant species in all the collected mallard faecal samples ($n = 251$), as a function of the number of days elapsed between sample collection and median flowering time of plant species recorded in a faecal sample. Median flowering time was calculated as the weighted average of flowering dates of species present in each faecal sample, with flowering dates being weighted by the number of seeds recovered of each species. Solid lines represent predictions from generalized linear models (see Supporting Information Table S3), while dashed lines represent their 95% confidence intervals. Each dot represents a sample, and only samples containing at least one seed of a submerged/emergent/terrestrial plant are shown. When samples (i.e., dots) coincide, they are represented by sunflowers, with the number of petals indicating the number of samples
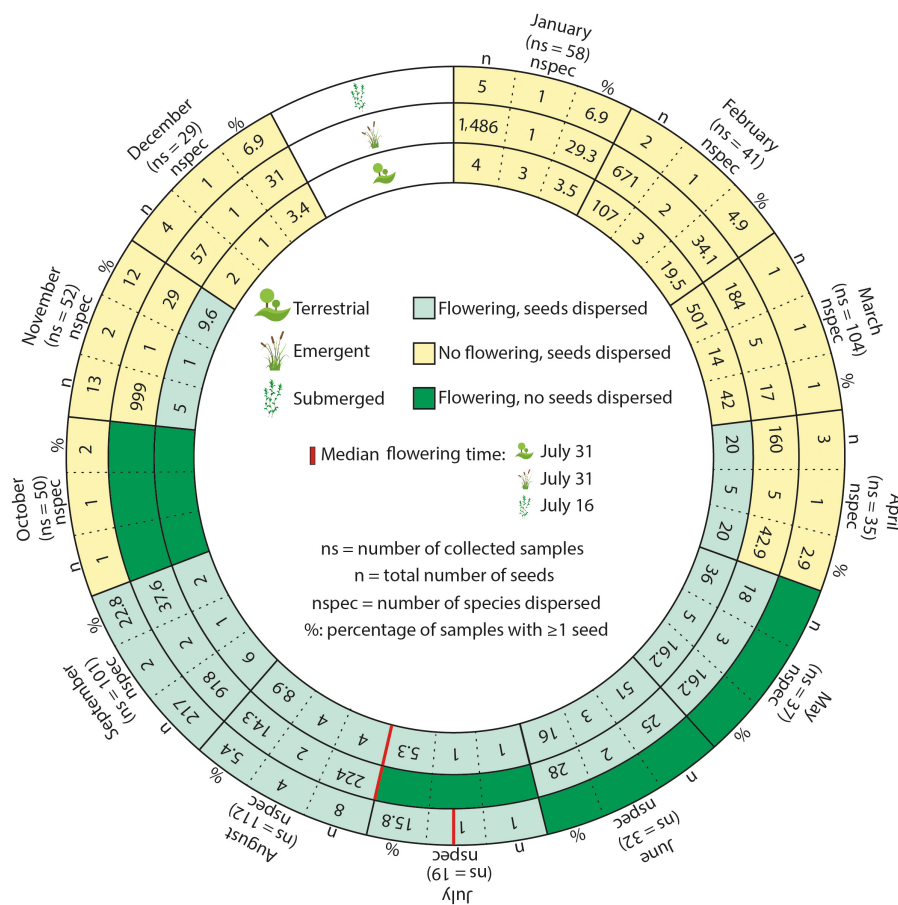

FIGURE 3 Summary of the monthly number of seeds and plant species recovered from mallard faecal samples for submerged, emergent and terrestrial plants in relation to flowering times
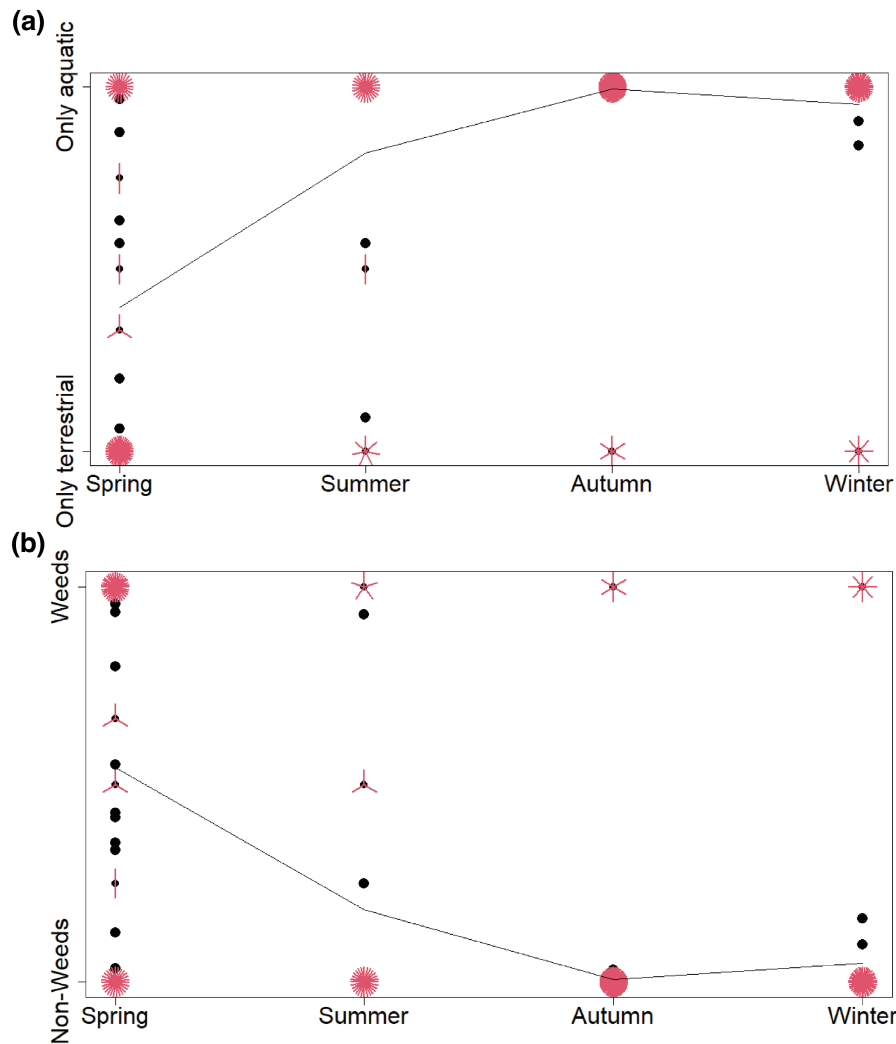
FIGURE 4 Sunflower diagrams showing (a) variation in the proportions of aquatic and terrestrial plant seeds in each faecal sample between seasons and (b) variation in the proportion of weed and non-weed seeds in faeces between seasons. The black dots represent samples with at least one seed from aquatic/terrestrial plants or weed/non-weed species. When samples (i.e., dots) coincide, they are represented by sunflowers, with the number of petals indicating the number of samples

ducks (Almeida et al., 2022; Soons et al., 2016). Even for some terrestrial plants (e.g., *C. glaucum*), ducks seem to be predictable dispersal vectors of an important fraction of seeds, and thus waterbird endozoochory needs to be recognized as a mainstream mechanism worthy of further research (see also Martín-Vélez, van Leeuwen, et al., 2021 for predictable weed dispersal by gulls). The majority of species we recorded had hydrochory and barochory (unassisted) dispersal syndromes, yet such dispersal mechanisms disperse seeds over much shorter distances than endozoochory (Bullock et al., 2017), with no capacity to move plants between catchment areas. The assignment of so many plants dispersed by mallards to the barochory syndrome (10 of 35 species) illustrates how the vectors with perhaps the best potential for long-distance dispersal (LDD) are dispersing plants assumed to have no capacity to disperse more than a few metres. The only species we recorded that has a fleshy fruit (and hence an endozoochory dispersal syndrome)

was the Russian olive (*Elaeagnus angustifolia*). Endozoochory of terrestrial plants with abiotic syndromes by birds can no longer be dismissed as occasional, rare events that are impractical to study in the field. Many previous studies predicting plant dispersal based on morphological dispersal syndromes overlooked such dispersal processes, and their results are thus unreliable (Green et al., 2022; Martín-Vélez, van Leeuwen, et al., 2021). Of 35 plant species detected in mallard faecal samples in this study we found five (14%) that had not been previously detected in the diets of European Anatidae, and a further three species not previously recorded in the diet of mallards (Almeida et al., 2022, Table 2). This underlines how little we still know about endozoochory by waterfowl, and which plant species are dispersed. The high proportion (nine of 33) of species we recorded as only a single seed also suggests major sampling error, and suggests that many more plant species will be dispersed by mallards from our study area in small numbers.

4.2 | Movements of seed dispersers

Ducks move continuously and do not feed at the exact spots where we collected samples, and thus all seeds recorded were dispersed away from their parent plants. As well as local dispersal within the lake and its shoreline, we regularly saw mallards flying into and away from the lake, and monthly changes in the number of mallards at the lake indicate strong migratory patterns (Supporting Information Figure S3). Outside migration periods, mallards undergo extensive daily movements often exceeding 10 km (Bengtsson et al., 2014; Kleyheeg, van Dijk, et al., 2017), and even breeding mallards move and disperse seeds between different wetlands (Bartel et al., 2018). At least 60% of mallards breeding in Hungary migrate outside the country outside the breeding period, and these birds migrate over distances from 500 to 2,300 km (Liker & Nagy, 2009). Modelling has already demonstrated that mallards disperse seeds by endozoochory over hundreds of km during their migrations, with maxima of 1,600 km (Kleyheeg et al., 2019; Viana et al., 2013). Although we found evidence for high rates of seed dispersal during spring migration, the total number of mallards undergoing spring migration is lower than for autumn (Supporting Information Figure S3), due to overwintering mortality. Ringing data show the migratory movements of mallards to and from Hungary, and resulting seed dispersal, do not correspond to a single, discrete flyway (Figure 1). In autumn, many arrive in Hungary from the north-northeast of Europe and then continue their migrations to wintering grounds in the eastern Mediterranean and Black Sea regions (Scott & Rose, 1996). These birds are part of a population of nearly one and a half million mallards in Eastern and Central Europe (Wetlands International, 2022).

4.3 | Seasonal variation in seed dispersal and link with phenology

The number of seeds in faeces was high in all months, showing that mallards are dispersing plant seeds continuously throughout the year (Figure 3). The germinability of seeds was tested under standardized conditions, leading to non-favourable conditions for the diverse set of species, thus it is likely that many viable seeds did not germinate (Brochet, Guillemain, Gauthier-Clerc, et al., 2010). Moreover, the huge variety of species with multiple dormancy strategies further decreases the chance of germination in standardized conditions. The seed prevalence in our samples is similar to previous duck studies (Lovas-Kiss, Vizi, et al., 2018; van Leeuwen et al., 2012). The high number of seeds in our spring samples contradicts earlier suggestions that seed dispersal during spring waterfowl migration would be strongly limited because migration precedes seed production (Clausen et al., 2002).

During the spring period, terrestrial species were predominant among plants dispersed, both in terms of species richness and seed abundance (Figure 3). For the rest of the year, seeds of emergent (typified by *S. litoralis*) and submerged (typified by *Potamogeton pectinatus*) aquatic plants were dominant in samples (Figure 3). β-diversity was greatest in spring, as expected given the high number

of rare, terrestrial species recorded only in that season. Similar seasonal patterns may be expected for other temperate dabbling ducks, but may differ in other waterfowl guilds, since herbivorous geese are more likely to ingest terrestrial seeds, and diving ducks are more likely to ingest seeds of submerged plants (Almeida et al., 2022). Previous studies using seeds fed to captive ducks showed that gut passage promotes earlier germination and faster establishment of *P. pectinatus* (Figuerola et al., 2005), and increases germinability of *S. litoralis* at favourable salinities (Espinar et al., 2004). The strong dispersal relationships between dabbling ducks and these aquatics are clearly mutualisms (Connor, 1995), although they are overlooked in the literature, which focuses on mutualistic frugivore interactions (van der Wall & Moore, 2016).

Unfortunately, there is limited information about the delay between flowering time and seed production but, for the plant species recorded, this delay is approximately 1 month (authors, personal observations). Only for submerged plants did we find evidence that endozoochory and seed production are strongly coupled, with an evident decline in dispersal rates in the months after seed production is completed. For emergent and terrestrial plants, endozoochory rates peaked several months after seed production. The different relationships between flowering time and seed ingestion for these three groups are consistent with different feeding methods used by mallards. Mallards prefer to forage at the surface when seeds or other food items are available there, switching to feeding under the water in winter, and at progressively greater depths as food resources in shallow areas are consumed (Green, 1998; Guillemain et al., 2002; Thomas, 1980, 1982).

Submerged plants are grazed by ducks, so their seeds are often ingested with the leaves before they are released. When released, they float for days or weeks, and are then directly eaten by surface-feeding mallards, as are the seeds of emergent plants (whose harder leaves are not eaten). Eventually losing their buoyancy, remaining seeds sink into the sediments where they remain available to mallards, which can upend to feed at depths of up to 40 cm (Green, 1998). The lake water level also reaches its lowest point in autumn and winter, which means that large areas close to the shoreline are an ideal depth for feeding in sediments. Seeds of terrestrial plants may originate from well away from the lake and are particularly likely to be ingested from the seed bank in sediments, after being blown or washed into the lake from its catchment area. Species with a persistent seed bank are more likely to be dispersed in this way, since their probability of ingestion increases over time. This may partly explain why most terrestrial plants dispersed were classified as weed species (Table 2), since persistent seed banks are a key trait of weediness.

Total abundance of seeds in our samples was highest in autumn and winter. Previous studies have shown seasonality in the composition of the diet of mallards, with a higher food diversity and relatively more invertebrates during the breeding period in spring (Dessborn et al., 2011; Krapu & Reinecke, 1992; Toufar et al., 1987). When feeding largely on invertebrates, seeds are more likely to survive gut passage than when plants are the main food source (Kleyheeg et al., 2018). Greater seed survival may partly explain why we

recorded higher species richness among seeds dispersed in spring, while the fewest species were found in autumn and winter, which can be explained by the alternation of the food base.

Our finding that more plant species are likely to be dispersed by ducks in spring contrasts with findings for frugivorous birds. González-Varo et al. (2021) found strong dispersal limitation for fleshy-fruited plants in the spring during the northward migration, which is vital for enabling plants to change their distributions in response to global heating. This is a consequence of strong coupling between fleshy-fruit production and endozoochory, since these birds ingest fruits directly from the parent plant. In contrast, our results suggest that migratory ducks may make a vital contribution to the resilience of aquatic and other dry-fruited plant species to climate change. Models by Viana (2017) confirmed that migrating mallards can disperse seeds fast enough to keep pace with climate change.

4.4 | Implications for dispersal of alien invasive species

As well as being key LDD vectors for native plants, waterfowl can also aid the spread of alien plants (Green, 2016), as illustrated by the four alien species recorded in our study. All four are invasive weeds worldwide whose dispersal by migratory ducks is of concern, and some are also dispersed by other waterbirds in agricultural habitats (Martín-Vélez, Lovas-Kiss, et al., 2021). The Russian olive (*Elaeagnus angustifolia*) is rapidly expanding in North American riparian and foreshore ecosystems, where it can have dramatic impacts on ecosystem structure and function (Collette & Pither, 2015). The Canada horseweed (*Conyza canadensis*) is generally assumed to disperse by wind (Holm et al., 1997; Julve, 1998), has herbicide resistant populations, and can cause damage to more than 40 crops (CABI, 2022; Holm et al., 1997). The redroot pigweed (*Amaranthus retroflexus*) is among the world's worst weed species, reported in 60 crops in 70 countries, and can cause yield reductions of up to 90% (Costea et al., 2004; Holm et al., 1997). The prostrate pigweed (*Amaranthus blitoides*) is known to impact yields of pinto beans (*Phaseolus vulgaris*), potato (*Solanum tuberosum*) and cotton (*Gossypium hirsutum*) in North America (Costea & Tardif, 2003). Moreover, almost every other species dispersed by mallards (Table 2) can be considered alien or naturalized somewhere in the world (van Kleunen et al., 2019). Hence, in other parts of their extensive range across the Northern Hemisphere, mallards are likely to be dispersal vectors for these same plant species, contributing to their expansion in their alien ranges.

5 | CONCLUSION

Our work provides key insights into the endozoochory of different plants by waterbirds over the annual cycle. It reinforces the need for a new paradigm in plant dispersal research, in which morphological dispersal syndromes are replaced by renewed attempts to understand the importance of animal vectors (Green et al., 2022). This study has focused on mallards as one of the most widespread waterbirds, but similarly detailed studies are needed for other migratory waterbirds. In future studies of seed dispersal networks for non-frugivorous vectors, understanding seasonality should be a priority.

CONFLICT OF INTEREST

The authors have declared no conflicts of interest for this article.

DATA AVAILABILITY STATEMENT

All the data are available at https://doi.org/10.6084/m9.figshare.21197272.v1.

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BIOSKETCH

Renáta Urgyán is an MSc student. Her research focuses on seed dispersal of various plants by different waterbirds. Her current research aims to establish how propagule dispersal by mallards and its seasonality can affect plant communities.

SUPPORTING INFORMATION

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

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