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The role of migratory ducks in the long-distance dispersal of native plants and the spread of exotic plants in Europe

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Little is known about the role of migratory waterfowl in the long-distance dispersal (LDD) of seeds. We studied the gut contents of 42 teals *Anas crecca* collected in the Camargue, southern France, and found intact seeds of 16 species. There was no relationship between the probability that a given seed species was found intact in the lower gut, and the seed hardness or size. The number of seeds found in the oesophagus and gizzard (a measure of ingestion rate) was the only significant predictor of the occurrence of intact seeds in the lower gut, so studies of waterfowl diet can be used as surrogates of dispersal potential. In a literature review, we identified 223 seed species recorded in 25 diet studies of teal, pintail *Anas acuta*, wigeon *A. penelope* or mallard *A. platyrhynchos* in Europe. We considered whether limited species distribution reduces the chances that a seed can be carried to suitable habitat following LDD. Overall, 72% of plant species recorded in duck diets in southern Europe (36 of 50) were also recorded in the north, whereas 97% of species recorded in duck diets in the north (137 of 141) were also recorded in the south. This suggests a great potential for LDD, since most dispersed plants species occur throughout the migratory range of ducks. Migratory ducks are important vectors for both terrestrial and aquatic plant species, even those lacking the fleshy fruits or hooks typically used to identify seeds dispersed by birds. Finally, we show ducks are important vectors of exotic plant species. We identified 14 alien to Europe and 44 native to Europe but introduced to some European countries whose seeds have been recorded in duck diet.

In recent years, there has been a growing interest in the potential role that seed dispersal by waterfowl (ducks, geese and swans) plays in the establishment and maintenance of plant communities in aquatic habitats (Green et al. 2008, Soons et al. 2008, Wongsriphuek et al. 2008). Waterfowl can transport plant propagules either in their guts (endozoochory, or internal dispersal) or attached to their bodies (epizoochory, or external dispersal) (Figuerola and Green 2002a). Waterfowl are abundant, widely distributed across the world's wetlands and highly mobile at local, regional and continental scales, often undergoing long-distance migrations (Wetlands International 2006). The importance of plant seeds in their diet makes endozoochory particularly likely (Green et al. 2002), and for some angiosperms it has been shown that seeds can survive gut passage intact and germinate effectively, even after being retained in the gut long enough to be moved a great distance during migration (Pollux et al. 2005, Soons et al. 2008, Wongsriphuek et al. 2008).

Nevertheless, it remains unclear whether waterfowl are important as seed dispersers for all the plant species whose seeds they consume, or only for a restricted number of species whose seeds are particularly resistant to digestion. Numerous studies show the importance of seeds in the diet of ducks (see Kear 2005, Baldassarre and Bolen 2006 for review), but without investigating whether they survive passage through the gut. Most diet studies are based on analysis of the content of the oesophagus and/or gizzard (i.e. the foregut) and do not consider whether food items persist beyond the muscular gizzard employed to crush them. Thus, to date it remains unclear whether or not presence of seeds of a given plant species in the diet of a waterfowl population is an indication that they are likely to be dispersed by it.

Furthermore, when a duck disperses a seed over a landscape or even larger scale (long-distance dispersal (LDD), Soons et al. 2008), there is almost no information available on the chance that the seed will be transported to an appropriate habitat. One potential barrier against LDD by waterfowl is that plant species can have limited latitudinal distributions that do not coincide with the broad range over which migratory waterfowl move. Another area of uncertainty is the potential that waterfowl have to disperse and spread alien plant species within their introduced range. Alien plants in Europe have an enormous conservation and economic impact (Brundu et al. 2001), yet we are unaware of any study addressing the role of aquatic birds in their spread.

The objectives of this paper are threefold. Firstly, we inspect the gut contents of teal *Anas crecca* wintering in the Camargue (southern France) to assess whether data on the presence of seeds in the oesophagus or gizzard (as presented in studies of duck diet) are a useful indicator of their presence as intact seeds in the lower gut (i.e. those likely to be dispersed by endozoochory). The teal migrates in large numbers to and through the Camargue, where it feeds mainly on seeds (Tamisier and Dehorter 1999). We also test if survival of passage through the gizzard is dependent on seed size or seed hardness.

Secondly, we consider to what extent the potential for LDD by ducks in Europe is limited by the restricted distribution of the plant species whose seeds they consume. For this purpose we use a literature review of the diet of four abundant migratory ducks that are widespread across Europe: the mallard *A. platyrhynchos*, pintail *A. acuta*, wigeon *A. penelope* and teal. As a measure of the possibility that a seed can be dispersed to a suitable area after a long-distance movement, we consider the chances that a species recorded in the diet of ducks in northern Europe is also found in southern Europe, and vice versa. The above four duck species make regular movements between northern and southern Europe during spring and autumn migrations (Wetlands International 2006).

Thirdly, based on the same literature review, we consider the potential role of migratory ducks in the spread of non-native plant species within Europe, by quantifying how many alien plants have their seeds recorded in duck diet.

Materials and methods

Analysis of teal gut samples

Digestive tracts ($n = 42$) were collected from teal hunted from September 2006 to January 2007 in six different hunting estates in the Camargue. The digestive tract is composed of five sections: the oesophagus, the gizzard, the intestines, the caeca and the rectum. For each section, intact seeds were counted under a binocular microscope and identified using Campredon et al. (1982), Cappers et al. (2006) and a reference collection from the Camargue. As no seed was ever found in the caeca, this part was not taken into account for this study. Data for intestine and rectum (I + RE) were combined owing to the small number of seeds recorded. If seeds pass the gizzard intact, they are likely to survive until defecation (Charalambidou and Santamaría 2002).

As the volume of the gizzard and the amount of grit (small stones or sand swallowed by birds to aid digestion) held within may also influence the probability that a seed is broken within the gizzard (DeVlaming and Proctor 1968, Figuerola et al. 2002), grit was later separated from food items in the gizzard, dried at room temperature, and weighed to the nearest 0.001 g. Gizzard volume was measured by volumetric displacement within a measuring cylinder.

Seed hardness was measured using a small device, used to measure manually hardness of soil (Lepont équipements, France), which applied increasing pressure from 0.75 to 10.00 kg cm^{-2}, at intervals of 0.25 kg cm^{-2} until a seed cracked. Seed size (maximum length) was measured on graph paper under a binocular microscope, to the nearest 0.02 mm. For both parameters, ten seeds per species (taken from the oesophagus) were measured. Median values were used in further analyses.

Statistical analyses

For 16 seed species which were present in the digestive tract of more than five birds and of which the total seed number was greater than five, a logistic regression was carried out with a binomial error distribution to test if the presence or absence of intact seeds in the lower gut (I + RE) of individual teal was related to the combined number of intact seeds in the oesophagus and gizzard (O + G), the grit mass (Grit) and the gizzard volume (VolG). We analysed presence or absence rather than the number of seeds present owing to the high proportion of zeros. We summed O + G because the number of intact seeds in the oesophagus was correlated with the number in the gizzard (Spearman test, $r_s = 0.327$, $p < 0.001$).

Initial models were conducted for the presence/absence of individual seed species (results not shown, except for *Eleocharis palustris*), but their statistical power was very limited since no species was present in the I + RE of more than five birds. We therefore analysed the total number of intact seeds for all species combined. To compare different models, we used the AIC corrected for small sample size (AICc), because the ratio of the sample size ($n = 42$) to the number of explanatory variables ($p = 3$) was < 40 (Burnham and Anderson 2002). The best model was the one with the smallest AIC value. However, if the difference of AICc (ΔAICc) between two models was < 2, they were considered equivalent (McCullagh and Nelder 1989).

To test the relationship between seed size, hardness and seed survival, data from different individual birds were pooled by seed species (Table 2). Spearman correlations were conducted between the percentage of all intact seeds found in I + RE, and size or hardness. R software (ver. 2.8.0) was used for all statistical analyses (R Development Core Team 2008).

Literature review of duck diet studies

We reviewed studies about the diet of four migratory duck species in Europe in which at least five seed species were identified in their digestive tract (Table 1). We arbitrarily defined three categories of location for the studies: studies carried out in northern (United Kingdom, Denmark and Sweden), southern (Spain, Portugal, Greece and the French

Table 1. Location and duck species for each diet study used in the literature review (N: northern, S: southern, M: middle Europe).

Code	Reference	Location	Duck species
[1]	Birger (1907)	Sweden (N)	mallard, teal, wigeon
[2]	Campredon (1984)	Southern France (S)	wigeon
[3]	Danell and Sjöberg (1980)	Sweden (N)	mallard, pintail, teal, wigeon
[4]	Karmiris and Kazantzidis (2007)	Greece (S)	mallard, pintail, teal, wigeon
[5]	Kiss et al. (1984)	Rumania (M)	mallard
[6]	Lanchon-Aubrais (1992)	France (M)	mallard
[7]	Mazzuchi (1971)	Switzerland (M)	teal
[8]	Mouronval et al. (2007)	France (M)	mallard, teal
[9]	Olney (1962)	UK (N)	mallard
[10]	Olney (1963)	UK (N)	teal
[11]	Olney (1964)	UK (N)	mallard
[12]	Olney (1965)	UK (N)	mallard
[13]	Owen and Thomas (1979)	UK (N)	wigeon
[14]	Pirot (1981)	Southern France (S)	mallard, pintail, teal
[15]	Rodrigues (1998)	Portugal (S)	mallard
[16]	Rodrigues and Ferreira (1993)	Portugal (S)	mallard
[17]	Rodrigues et al. (2002)	Portugal (S)	mallard
[18]	Schricke (1983)	France (M)	teal
[19]	Spärck (1947)	Denmark (N)	mallard, pintail, teal, wigeon
[20]	Sterbetz (1967)	Hungary (M)	mallard
[21]	Street (1977)	UK (N)	mallard
[22]	Suarez-R and Urios (1999)	Spain (S)	mallard, pintail, teal, wigeon
[23]	Tamisier (1971)	Southern France (S)	teal
[24]	Thomas (1982)	UK (N)	mallard, pintail, teal
[25]	Brochet and Mateo unpubl.[a]	Spain (S)	mallard, pintail, teal, wigeon

[a]: Data from Ebro Delta, samples were from birds described by Mateo et al. (2000).

Camargue) or middle Europe (more northerly parts of France, Rumania, Switzerland and Hungary).

We only used studies carried out in northern or southern Europe (n = 19) to investigate whether or not plant species recorded in the diet in the north also occur in the south and vice-versa. The country or island of distribution of seed species was determined using the Flora Europaea (Royal Botanic Garden Edinburgh 2008). We arbitrary considered plant species to be recorded in the north if they are present in any of the following countries: United Kingdom (UK), Denmark, Sweden, Finland, Norway, Iceland, Estonia, Lithuania or Latvia. We considered them to be recorded in the south if present in any of the following countries: Spain, Portugal, Italy, Greece or Turkey. The minimum distance between northern and southern blocks (i.e. southern tip of the UK and the northern tip of Italy) in a straight line is 750 km. We considered a plant species to be distributed throughout Europe if it was observed in at least one of these countries in the north and one from the south. For each diet study carried out in the north, we determined the proportion of plant species present or absent in the south. Likewise, for each diet study carried out in the south, we determined the proportion of plant species present or absent in the north. For studies from the two regions, we

Table 2. Hardness and size of the seed species in teal guts, together with their abundance (data pooled for all teal examined, n = 42).

Seed species	Hardness (kg cm^{-2})	Size (mm)	Total number of intact seed species in all guts	Total number of intact seed species in I+RE[a]	%[b] of intact seed in I+RE[a]
Chara sp.	0.750	0.58	1148	33	2.87
Echinochloa crus-galli	2.000	3.92	3818	19	0.50
Eleocharis palustris	2.250	1.18	474	4	0.84
Heteranthera reniformis	0.875	0.64	1186	3	0.25
Myriophyllum spicatum	2.000	1.84	284	2	0.70
Najas gracillima	1.250	2.36	41	0	0.00
Najas minor	1.000	2.06	895	0	0.00
Phragmites australis	1.375	1.82	102	0	0.00
Polygonum lapathifolium	5.250	2.10	37	1	2.70
Polygonum sp.	7.500	2.08	236	0	0.00
Potamogeton pectinatus	4.750	3.40	31	0	0.00
Potamogeton pusillus	2.875	1.55	2041	8	0.39
Rubus sp.	2.125	2.56	14	1	7.14
Schoenoplectus mucronatus	3.000	1.90	484	13	2.69
Scirpus maritimus	8.125	2.48	1418	8	0.56
Zannichellia sp.	2.000	2.38	309	0	0.00

[a]: Intestines and rectum combined.
[b]: This figure does not reflect the % of seeds ingested that survive gut passage. Had the birds not been shot, many of the seeds observed in the oesophagus and gizzard are likely to have survived.

then compared the proportions of plant species with widespread distributions, using a Mann Whitney U test.

All 25 available diet studies were examined to identify plant species in duck diet originating from outside Europe, or native to some European countries but introduced into others. The status of each plant species (native or introduced) was taken from the Flora Europaea (Royal Botanic Garden Edinburgh 2008). We compared the numbers of species introduced only to the north or only to the south using sign tests (Siegel and Castellan 1988).

Results

Seed digestion

For the logistic regression testing the presence or absence of intact seeds in the lower gut (I + RE) of individual teal, the total number of seeds in the upper gut (O + G) was the only significant variable in the best models (Table 3); thus the more seeds in the upper gut, the greater the chance of some seeds passing intact into the lower gut. Similarly, the number of *E. palustris* seeds in the upper gut was significantly and positively related to the number in the lower gut ($p = 0.027$).

No significant correlation was found among plant species between the percentage of intact seeds found in I + RE and seed hardness ($r_s = 0.126$, $p = 0.642$) or size ($r_s = -0.163$, $p = 0.546$). This suggests that there are only weak differences between seed species in their rate of survival of gut passage, and that all seed species recorded in the gizzard or oesophagus are likely to be dispersed by teal. There was a non-significant positive correlation between the hardness and size of seeds ($r_s = 0.419$, $p = 0.106$).

Potential for long-distance dispersal

After reviewing duck diet studies from northern and southern Europe, information was available for 173 different seed species recorded in the diet. The proportion of seed species restricted to a given region (Table 4) was consistently higher in the south than in the north (Mann Whitney U test, $W = 0.5$, $p < 0.001$). Overall, 72% of plant species occurring in duck diets in the south (36 of 50) were also recorded in the north, whereas 97% of species occurring in duck diets in the north (137 of 141) were also recorded in the south.

Dispersal of exotic species

We identified a total of 223 different seed species recorded in all duck diet studies (i.e. including those from central Europe, Supplementary material). Among them, 14 are alien to Europe, of which 8 have been introduced in the south, and 6 both in the north and south. The number of species alien to Europe only introduced to the south was significantly higher than that only introduced into the north (sign test, $z = 2.475$, $p = 0.007$).

Another 44 species are native to Europe but have been introduced into at least one European country, either only in the north (32), only in the south (4), in both north and south (4) or in central Europe (4) (Table 5). The number of European species only introduced to non-native countries in the north was significantly higher than the number only introduced into the south (sign test, $z = 4.056$, $p < 0.001$). Of these 44 species, five species were recorded in duck diet in non-native countries (Table 5).

Discussion

Study of teal gut contents

The resistance of seeds to avian digestive processes can be expected to depend mainly on the nature of the seed coat, especially its resistance to mechanical crushing in the gizzard (DeVlaming and Proctor 1968, Figuerola et al. 2002). It may therefore be expected that the probability of seed passing intact through the digestive tract increases with seed hardness, and decreases with increasing grit mass or gizzard size. Small size might also be expected to confer an advantage, since large seeds may become lodged within the gizzard until eventually crushed, while the smaller ones may pass through the gizzard more quickly (DeVlaming and Proctor 1968, Figuerola et al. 2002, Holt Mueller and van der Valk 2002, Soons et al. 2008). However, our study of teal gut contents found no evidence for such relationships, suggesting that there were only weak differences in "digestibility" between the seed species found in the guts we examined, and that all seeds consumed have a similar probability of being dispersed. The only significant predictor of the presence of intact seeds in the lower gut was their abundance in the foregut.

Although ducks ingest seeds as food items, many seeds escape digestion and the proportion of seeds broken in the gizzard decreases as the rate of ingestion increases (Figuerola et al. 2002). Further support comes from De Vlaming and

Table 3. Null and best models for the logistic regression of presence–absence of seeds of any species in the intestines and rectum of each teal, showing the estimate (β) and standard-error (SE) for each variable. Models include the variables: O+G, combined number of intact seeds in the oesophagus and gizzard; Grit, grit mass; VolG, gizzard volume.

Models	ΔAICc	O+G			Grit			VolG		
		β	SE	p	β	SE	p	β	SE	p
O+G	0.00	0.005	0.002	0.044						
O+G+Grit	0.54	0.006	0.003	0.036	1.115	1.235	0.367			
O+G+VolG	1.40	0.005	0.003	0.048				−0.184	0.196	0.348
O+G+Grit+VolG	1.97	0.006	0.003	0.040	1.142	1.249	0.360	−0.200	0.200	0.323
Null model	7.56									

Table 4. Distribution of seed species (whether native or not) found in duck diet studies from northern or southern Europe, according to Flora Europeae (data from different duck species in a given study were combined).

Study region	Study reference[a]	Number of seed species	Number of species distributed in Europe			% in common
			only in the south	only in the north	throughout	
North	[1]	11	0	1	10	90.9
	[3]	7	0	1	6	85.7
	[9]	14	0	0	14	100
	[10]	94	0	1	93	98.9
	[11]	45	0	2	43	95.6
	[12]	22	0	0	22	100
	[13]	19	0	0	19	100
	[19]	5	0	0	5	100
	[21]	8	0	0	8	100
	[24]	21	0	0	21	100
South	[2]	20	5	0	15	75
	[4]	7	1	0	6	85.7
	[14]	21	6	0	15	71.4
	[15]	5	2	0	3	60
	[16]	5	2	0	3	60
	[17]	5	3	0	2	40
	[22]	5	3	0	2	40
	[23]	15	5	0	15	66.7
	[25]	28	8	0	20	71.4

[a]: See Table 1.

Proctor (1968), Holt-Mueller and Van der Valk (2002), Pollux et al. (2005), Soons et al. (2008) and Wongsriphuek et al. (2008) who experimentally fed seeds of different moist soil and aquatic plants to mallards and retrieved seeds from faeces. They confirmed seed viability following gut passage for 51 of 54 species studied. Furthermore, seeds of one of the other three species were retrieved intact, although they failed to germinate. We can therefore assume that the presence of a seed species in the diet of *Anas* spp. dabbling duck species is a good indication that seed dispersal is likely to occur. Given that field studies quantifying the viable seeds carried inside waterfowl or excreted in their faeces are scarce (Figuerola and Green 2002a, Green et al. 2008), this allows us to use diet data from the literature as a surrogate of dispersal potential for comparative studies.

Duck species with heavier gizzards destroy a higher proportion of the seeds ingested, and the relatively small gizzard of teal is less efficient at breaking up seeds than that of larger species (Proctor and Malone 1965, Proctor et al. 1967, Figuerola et al. 2002). These studies were performed at the interspecific level, in contrast to our intraspecific study. Consequently the variability in gizzard size was much reduced in our study. Moreover, our failure to find a relationship between grit mass or gizzard volume and seed survival may have been due to type II error associated with the small chance of observing seeds in the lower gut of these relatively small ducks at a given moment in time. We are not aware of any other studies comparing the effect of gizzard or grit mass on seed survival within a species.

Previous attempts to relate seed survival to seed hardness have given contradictory results. Wongsriphuek et al. (2008) reported a positive correlation between the proportion of seeds remaining intact after passage through mallard guts and seed fibre content. However, Holt Mueller and van der Valk (2002) found an opposing trend with lignin content. Wongsriphuek et al. (2008) reported a negative correlation between seed fibre content and the proportion of intact seeds germinating after passage through mallard guts. In contrast, Holt Mueller and van der Valk 2002 found a positive correlation with lignin content. Seed coat thickness probably has more influence on germination patterns after gut passage than on seed survival (Traveset 1998). Soons et al. (2008) found an increase of germination after gut passage for species with a thick seed coat and a decrease for species with a thin seed coat. However, the germination response to gut passage can change according to salinity, and most experimental studies have not taken this into account (Espinar et al. 2004). As in the current study, Wongsriphuek et al. (2008) failed to find a clear relationship between survival and seed size. However, Soons et al. (2008) found that smaller seeds are retrieved in greater number, pass faster through the digestive tract and germinate better. One potential explanation for the different results is the much smaller range of seed sizes found in teal guts than that fed experimentally to mallards by Soons et al. (2008). Another possible explanation is the difference between the duck species used (mallard versus teal), although captive studies have found no evidence of a difference between these species in seed retrieval (Charalambidou et al. 2003, Pollux et al. 2005). Our measure of seed survival was relatively poor compared with the gradual retrieval of seeds from faeces after feeding captive birds, but we are confident that this does not explain our lack of an effect of seed size or hardness because we have found similar results in just such a captive experiment with teal (Brochet et al. unpubl.).

Potential for long-distance dispersal

Of the 223 seed species recorded in our review of the diet of dabbling ducks, 91% have a wide geographic distribution, including both southern and northern Europe. This suggests that a restricted distribution of plant species may not be a major barrier to LDD of seeds by ducks. The duck species studied are capable of making non-stop migratory

Table 5. Distribution of seed species found in duck diet which are alien to Europe or which are introduced in at least one European country, according to Flora Europeae (C: central; N: northern; S: southern, T: throughout Europe). Central Europe corresponds to 3 countries: Austria, Germany and Switzerland.

Seed family	Seed species	Number of countries where the species is introduced/ present	Introduction area	Distribution area	Study reference (see Table 1)
Amaranthaceae	*Amaranthus albus*[a]	24/24	T	T	[5]
	Amaranthus retroflexus[a, c]	27/27	T	T	[5]
Betulaceae	*Alnus glutinosa*	1/30	S	T	[6]; [7]; [9]; [10]; [12]; [21]
	Alnus incana	7/29	T	T	[7] [d]
Caprifoliaceae	*Sambucus nigra*[c]	3/30	N	T	[7]; [10]; [13]
	Sambucus racemosa	5/25	N	T	[7]
	Viburnum lantana	2/19	N	T	[5]
Chenopodiaceae	*Chenopodium album*[c]	2/32	N	T	[7]; [10]; [11]; [12]; [21]
Compositae	*Cirsium arvense*[c]	2/32	N	T	[24]
	Helianthus annuus[a, b]	14/14	S	S	[5]
Elaeagnaceae	*Elaeagnus angustifolia*[a, c]	16/16	T	T	[5]; [14]
Gramineae	*Alopecurus myosuroides*	14/28	N	T	[10]
	Alopecurus pratensis	2/32	N	T	[10]; [13]
	Bromus sterilis	4/30	N	T	[12]
	Cynodon dactylon[c]	1/20	C	T	[10]
	Digitaria sanguinalis	12/25	N	T	[15]; [16];[17]
	Echinochloa crus-galli[c]	13/26	N	T	[2]; [5]; [15]; [16]; [23]
	Festuca rubra	2/31	S	T	[10]; [13]
	Holcus lanatus	2/32	N	T	[10]; [12]; [13]
	Lolium multiflorum	16/26	N	T	[12] [d]
	Oryza sativa[a, b]	14/14	S	S	[2]; [14]; [15]; [16]; [17]; [20]; [23]; [25]
	Panicum miliaceum[a, c]	21/21	T	T	[20]
	Paspalum distichum[a, c]	4/4	S	S	[14]; [25]
	Paspalum paspalodes[a, c]	9/9	S	S	[15]; [16]; [17]
	Setaria italica[a]	15/15	S	S	[7]
	Setaria pumila[c]	9/24	N	T	[5]; [25]
	Setaria verticillata[c]	12/24	N	T	[25]
	Sorghum bicolour[a, b]	14/14	S	S	[22]
	Spartina townsendii	5/7	N	N	[10]; [11]
	Zea mays[a, b]	24/24	T	T	[5]; [19]; [20]
Labiatae	*Ajuga reptans*	1/30	N	T	[9]
Leguminosae	*Lotus uliginosus*	4/28	N	T	[10]
	Medicago lupulina	2/32	N	T	[25]
	Medicago sativa	1/32	N	T	[20]
	Trifolium campestre	2/31	N	T	[10]; [11]
	Trifolium pratense[c]	2/32	N	T	[10]; [11]
Lythraceae	*Lythrum salicaria*[c]	1/30	N	T	[7]
Malvaceae	*Althaea officinalis*[c]	1/24	C	T	[25]
Menyanthaceae	*Nymphoides peltata*[c]	3/26	N	T	[6]
Najadaceae	*Najas gracillima*[a, c]	1/1	S	S	[25]
Onagraceae	*Epilobium hirsutum*[c]	3/30	N	T	[10]
Papaveraceae	*Chelidonium majus*	1/30	N	T	[7]
Polygonaceae	*Polygonum aviculare*[c]	1/32	N	T	[5];[10]; [11]; [18]; [25]
	Polygonum minus[c]	1/28	S	T	[18]
	Rumex conglomeratus[c]	3/27	T	T	[10]; [12]; [13]; [24]
	Rumex crispus[c]	2/32	T	T	[9]; [10]; [13]; [24]
	Rumex pulcher[c]	2/17	C	T	[5]
Pontederiaceae	*Heteranthera reniformis*[a, c]	1/1	S	S	[25]
Ranunculaceae	*Ranunculus acris*[c]	2/31	T	T	[1]; [10]; [11]
	Ranunculus sardous[c]	1/25	N	T	[10]; [18]
Resedaceae	*Reseda lutea*	11/24	N	T	[20]
	Reseda luteola	11/26	N	T	[8]
Rubiaceae	*Galium tricornutum*	1/23	N	T	[11] [d]
Scrophulariaceae	*Linaria arvensis*	1/14	C	S	[7] [d]
	Veronica persica[a]	31/31	T	T	[11]
Solanaceae	*Solanum dulcamara*[c]	1/30	N	T	[7]
Umbelliferae	*Falcaria vulgaris*	5/23	N	T	[5]
Vitaceae	*Vitis vinifera*[b]	6/20	S	S	[6]; [25] [d]

[a]: Seed species alien to Europe; [b]: crop species; [c]: ricefield weeds according to Pieterse and Murphy (1990) and Marnotte et al. (2006); [d]: study in which the seeds of a species native to Europe were recorded in ducks outside the plant's native range.

flights of over 1000 km while carrying seeds within (Clausen et al. 2002, Green and Figuerola 2005). Millions of individual ducks migrate from north to south in Europe and back each year (Wetlands International 2006), so that even if the probability of LDD of a seed by an individual duck is very low, it is likely to be high at the population level. The number of dispersers is higher during the autumn, southwards migration, as the young of the year participate and many birds die during the winter period (Baldassarre and Bolen 2006).

Transport of a seed to an appropriate habitat after LDD provides no guarantee of establishment, although many plants have sufficient plasticity to survive over a broad latitudinal range (Santamaría et al. 2003). When transported to sites with existing populations, migrant seeds may be unable to compete with locally adapted populations (De Meester et al. 2002). However, under climate change predictions (Thuiller et al. 2005), LDD of seeds in a northerly direction is particularly important as plant species shift distributions in response to increased temperatures. Indeed, such northwards shifts are already underway for many species (Hughes 2000, Walther et al. 2005), and the ability to undergo LDD via birds will reduce extinction risk for plant species under rapid climate change (Brooker et al. 2007).We have shown that most plant species whose seeds are consumed by ducks in southern Europe are already present in the north, and northwards LDD of genotypes adapted to warmer temperatures may already be important. We found that a significantly higher proportion of seeds ingested by ducks in southern Europe are limited to those latitudes compared with the equivalent proportion in northern Europe. This is consistent with the higher plant diversity and endemicity at more southerly latitudes (Tutin et al. 1964). Thus, it is particularly likely that seed species ingested in northern Europe during autumn migration will remain within their range after LDD to the south.

It is striking that the majority of plants whose seeds were recorded in dabbling duck foreguts are not strictly aquatic, but are instead from moist soil or terrestrial plants (Supplementary material). Previous studies showed that waterbirds are responsible for dispersing aquatic species (Charalambidou and Santamaría 2002, Figuerola et al. 2003), but our review indicates that they are excellent vectors for terrestrial plants surrounding aquatic habitats or colonizing temporary waterbodies during their terrestrial phase (e.g. seasonally flooded grasslands, floodplains, etc.). Waterfowl can also disperse seeds directly into terrestrial habitats as they sometimes feed in them (e.g. in agricultural fields) and often defecate while roosting on land or when flying between aquatic habitats. Biogeographical studies of island flora also suggest that LDD by waterbirds is extremely important in the establishment of plants both in aquatic environments and their margins (McGlone et al. 2001).

In our review, we have only found a relatively small number of diet studies, each of which represents a snapshot in time of what ducks were ingesting in a given locality. In the same studies, many other seed species went unidentified owing to the lack of suitable reference keys and the high diversity of the plant species pool present in any study area. Most studies of waterbird diet fail to identify all the seeds present. Furthermore, we only reviewed data on the diet of a small number of waterfowl species across a limited proportion of their European range (see Kear 2005 for details of other species ingesting seeds). In addition, we have only addressed endozoochory whereas some plant species may be more likely to be dispersed by epizoochory (Ridley 1930, Figuerola and Green 2002b). Thus, our study is likely to underestimate the number of plant species undergoing LDD by waterfowl, and can be considered to be conservative.

Spread of exotic species

As far as we know, this is the first study to address the importance of waterbirds as vectors of alien plant species in Europe, though the spread of these invasive species is of growing concern (Brundu et al. 2001). Individual studies have previously shown waterfowl can potentially disperse seeds of aliens in the USA (Powers et al. 1978) and Australia (Green et al. 2008). Shorebirds in Europe have also been shown to potentially disperse seeds of plant species that are invasive aliens in other continents and non-native in some European countries (Sánchez et al. 2006). The importance of forest birds and passerines in the dispersal of terrestrial alien plants with fleshy fruits is already recognized (Buckley et al. 2006).

Within the diet of dabbling ducks, we recorded 14 species introduced from outside Europe (alien to Europe sensu Lambdon et al. 2008) and a higher number (44) of European plant species that are non-native in some European countries. These latter species also tend to be invasive aliens in other continents (Müller and Okuda 1998). These introductions of European species to other countries within Europe appear to have been made in an asymmetric way, with many more species being introduced from southern countries to the north than in the opposite direction. This is likely to be partly a reflection of the higher number of plant species present in, and restricted to, the south, i.e. the pool of species available for introduction to the north is much larger than that available for introduction from north to south. However, it may also reflect a greater historical tendency to introduce exotic plants in northern Europe deliberately or accidentally. According to Lambdon et al. (2008), the major pathways for introduction of European natives to other countries within Europe are intentional introductions for ornamental or horticultural purposes, or accidental introductions as seed contaminants. This asymmetry may also reflect the effects of urbanisation in creating warmer microclimates in northern countries that have permitted effective establishment of more southerly species. Such northwards range expansions can also be expected in response to climate change, waterbirds being one of the vectors facilitating such an expansion.

In contrast, we found the opposite geographical trend for the 14 species alien to Europe, with most being introduced into southern Europe. This is despite the fact that the pathways of introduction of these species and of European natives are thought to be similar (Lambdon et al. 2008). The main reason for our contrasting results is that some of the aliens to Europe are crop species only cultivated in southern Europe (3 of 14) and some others arrived in a shared pathway as contaminants of ricefields (4 of 14).

Our results suggest that greater attention should be paid to the potential role of LDD by waterbirds in the spread of alien plant species (including non-aquatic species). Until now, the importance of this pathway appears to have been underestimated in the literature on exotic plants. In their extensive review, Lambdon et al. (2008) make no mention of bird dispersal as a means of spread of alien plants. Even for seeds that are usually dispersed by other means over short distances, waterbirds may be responsible for LDD events of relative significance in the spread of exotics (Higgins et al. 2003, Sánchez et al. 2006). Furthermore, some plants are dispersed as fragments, and it has long been suggested that the spread of the aliens *Elodea canadensis* and *Azolla filicoides* in Europe has been largely facilitated by waterbirds (Ridley 1930).

The relative importance of endozoochory and epizoochory

In the dispersal literature, it has often been wrongly assumed that seed morphology is a reliable means of predicting dispersal mode, and that those with fleshy fruits are dispersed by endozoochory, those with sticky fruits, hooks or similar structures are dispersed by epizoochory, and other seed types are not vertebrate dispersed (McGlone et al. 2001, Prinzing et al. 2002). In fact, the majority of the seeds found in our review of duck diet (Supplementary material) meet neither of these criteria, notable exceptions being the alien Russian olive *Elaeagnus angustifolia* and the common grape vine *Vitis vinifera* (Table 5) which have fleshy fruits. Another related, mistaken assumption in many studies is that seeds lacking fleshy fruits must travel attached to birds rather than within their digestive system (McGlone et al. 2001, Řehounková and Prach 2008). Similarly, most seed types dispersed internally by emus *Dromaius novaehollandiae* have morphologies associated with other dispersal modes (Calviño-Cancela et al. 2006).

This overemphasis on epizoochory can be traced to Darwin (1859) and Ridley (1930), who both largely attributed LDD to feathers and muddy feet. Likewise, even though Carlquist (1967) recognized the potential of ducks to carry out LDD both by epizoochory and endozoochory, based on their morphology he proposed many genera to be dispersed by epizoochory which we now know to be readily transported internally by ducks (e.g. *Ruppia*, *Najas*, *Paspalum*, *Eleocharis*, *Ranunculus*, *Plantago*).

Absence of obvious morphological adaptations for bird dispersal in their seeds is one reason why waterbirds have been largely overlooked as vectors of alien plants. Not surprisingly given our results, the presence of fleshy or sticky fruits or of hooks can be a poor predictor of invasiveness (Prinzing et al. 2002), but this should not be interpreted as sound evidence that invasiveness is unrelated to the capacity to disperse via birds.

Conclusion

We have shown in this study that dabbling ducks have considerable potential to disperse seeds by endozoochory. Ducks can transport aquatic plants as well as terrestrial ones and seed morphology gives no reliable clue about which species can be dispersed internally by waterfowl. Most seed types ingested occur throughout the migratory ranges of ducks and thus can be readily dispersed during migrations. Limited geographic distribution is not a major barrier to the LDD of plants by waterfowl within Europe. Furthermore, the importance of endozoochory by migratory ducks in the spread of exotics has been largely overlooked. The role of these birds in changes in plant distribution in response to global change, and in promoting the spread of exotic species, merits greater attention in the future.

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References

Baldassarre, G. A. and Bolen, E. G. 2006. Waterfowl ecology and management, 2nd ed. – Krieger Publ.

Birger, S. 1907. Über endozoisxhe Samenverbreitung durch Vögel. – Sv. Bot. Tidskr. 1: 1–31.

Brooker, R. W. et al. 2007. Modelling species' range shifts in a changing climate: the impacts of biotic interactions, dispersal distance and the rate of climate change. – J. Theor. Biol. 245: 59–65.

Brundu, G. et al. 2001. Plant invasions: species ecology and ecosystem management. – Backhuys Publ.

Buckley, Y. M. et al. 2006. Management of plant invasions mediated by frugivore interactions. – J. Appl. Ecol. 43: 848–857.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information – theoretic approach, 2nd ed. – Springer.

Calviño-Cancela, M. et al. 2006. Emus as non-standard seed dispersers and their potential for long-distance dispersal. – Ecography 29: 632–640.

Campredon, P. 1984. Régime alimentaire du canard siffleur pendant son hivernage en Camargue. – L'Oiseau et R.F.O. 54: 189–200.

Campredon, S. et al. 1982. Manuel d'analyse des contenus stomacaux de canards et de foulques. – ONC.

Cappers, R. T. J. et al. 2006. Digital seed atlas of the Netherlands. – Barkhuis Publ.

Carlquist, S. 1967. The biota of long-distance dispersal. V. Plant dispersal to Pacific islands. – Bull. Torrey Bot. Club 94: 129–162.

Charalambidou, I. and Santamaría, L. 2002. Waterbirds as endozoochorous dispersers of aquatic organisms: a review of experimental evidence. – Acta Oecol. 23: 165–176.

Charalambidou, I. et al. 2003. Effect of ingestion by five avian dispersers on the retention time, retrieval and germination of *Ruppia maritima* seeds. – Funct. Ecol. 17: 747–753.

Clausen, P. et al. 2002. Long-distance endozoochorous dispersal of submerged macrophyte seeds by migratory waterbirds in northern Europe – a critical review of possibilities and limitations. – Acta Oecol. 23: 191–203.

Danell, K. and Sjöberg, K. 1980. Foods of wigeon, teal, mallard and pintail during the summer in the northern Swedish Lake. – Viltrevy 11: 141–167.

Darwin, C. 1859. On the origin of species by means of natural selection. – Murray.

De Meester, L. et al. 2002. The monopolization hypothesis and the dispersal-gene flow paradox in aquatic organisms. – Acta Oecol. 23: 121–135.

DeVlaming, V. and Proctor, V. W. 1968. Dispersal of aquatic organisms: viability of seeds recovered from the droppings of captive killdeer and mallard ducks. – Am. J. Bot. 55: 20–26.

Espinar, J. L. et al. 2004. Helophyte germination in a Mediterranean salt marsh: gut-passage by ducks changes seed response to salinity. – J. Veg. Sci. 15: 315–322.

Figuerola, J. and Green, A. J. 2002a. Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. – Freshwater Biol. 47: 483–494.

Figuerola, J. and Green, A. J. 2002b. How frequent is external transport of seeds and invertebrate eggs by waterbirds? A study in Donana, SW Spain. – Arch. Hydrobiol. 155: 557–565.

Figuerola, J. et al. 2002. Comparative dispersal effectiveness of wigeongrass seeds by waterfowl wintering in south-west Spain: quantitative and qualitative aspects. – J. Ecol. 90: 989–1001.

Figuerola, J. et al. 2003. Passive internal transport of aquatic organisms by waterfowl in Doñana, south-west Spain. – Global Ecol. Biogeogr. 12: 427–436.

Green, A. J. and Figuerola, J. 2005. Recent advances in the study of long-distance dispersal of aquatic invertebrates via birds. – Divers. Distrib. 11: 149–156.

Green, A. J. et al. 2002. Implications of waterbird ecology for the dispersal of aquatic organisms. – Acta Oecol. 23: 177–189.

Green, A. J. et al. 2008. The potential role of waterbirds in dispersing invertebrates and plants in arid Australia. – Freshwater Biol. 53: 380–392.

Higgins, S. I. et al. 2003. Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? – Ecology 84: 1945–1956.

Holt Mueller, M. and van der Valk, A. G. 2002. The potential role of ducks in wetland seed dispersal. – Wetlands 22: 170–178.

Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? – Trends Ecol. Evol. 15: 56–61.

Karmiris, I. and Kazantzidis, S. 2007. Wintering diet composition of selected wildfowl species in Greece. – 31st Annual Meeting of Waterbird Society, Barcelona.

Kear, J. 2005. Ducks, geese and swans (Vol. 1 and 2). – Oxford Univ. Press.

Kiss, J. B. et al. 1984. A duna-deltában (Románia) élö tökés (*Anas Platyrhynchos*) ès cigányrécék (*Aythya nyroca*) táplálékának vizsgálata. [A study of the foods of the mallard (*Anas platyrhynchos*) and of the Ferrouginosus duck (*Aythya nyroca*) in the Danube Delta (Roumania).]. – Puszta 2: 39–51.

Lambdon, P. W. et al. 2008. Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. – Preslia 80: 101–149.

Lanchon-Aubrais, E. 1992. Conséquence d'un apport artificel de nourriture sur le comportement d'un canard de surface: le Canard colvert (*Anas platyrhyncos*, L.) et d'un canard plongeur: le Fuligule milouin (*Aythya ferina*, L.) au lac de Grand-Lieu. – Univ. de Rennes I.

Marnotte, P. et al. 2006. Plantes des rizières de Camargue. – Cirad, CFR, PNRC.

Mateo, R. et al. 2000. Determinants of lead shot, rice, and grit ingestion in ducks and coots. – J. Wild. Manage. 64: 939–947.

Mazzuchi, L. 1971. Beitrag zur Nahrungsökologie in der Umgebung von Bern überwinternder Krinckenten *Anas crecca* L. – Ornithol Beob. 68: 161–178.

McCullagh, P. and Nelder, J. A. 1989. Generalized linear models, 2nd ed. – Chapman and Hall/CRC.

McGlone, M. S. et al. 2001. Endemism, species selection and the origin and distribution of the vascular plant flora of New Zealand. – J. Biogeogr. 28: 199–216.

Mouronval, J. B. et al. 2007. Diet of non-breeding wildfowl Anatidae and coot *Fulica atra* on the Perthois gravel pits, northeast France. – Wildfowl 57: 68–97.

Müller, N. and Okuda, S. 1998. Invasion of alien plants in floodplains – a comparison of Europe and Japan. – In: Starfinger, U. et al. (eds), Invasion of alien plants in floodplains – a comparison of Europe and Japan. Backhuys Publ., pp. 321–332.

Olney, P. J. S. 1962. The food habits of a hand-reared mallard population. – Ann. Rep. Wildfowl Trust 13: 119–125.

Olney, P. J. S. 1963. The food and feeding habits of teal *Anas crecca crecca* L. – Proc. Zool. Soc. Lond. 140: 169–210.

Olney, P. J. S. 1964. The food of mallard *Anas platyrhyncos platyrhyncos* collected from coastal and estuarine areas. – Proc. Zool. Soc. Lond. 142: 397–418.

Olney, P. J. S. 1965. Part II. The feeding ecology of local mallard and other wildfowl. – Ann. Rep. Wildfowl Trust 18: 47–54.

Owen, M. and Thomas, G. J. 1979. The feeding ecology and conservation of wigeon wintering at the Ouse Washes, England. – J. Appl. Ecol. 16: 795–809.

Pieterse, A. H. and Murphy, K. J. 1990. Aquatic weeds, the ecology and management of nuisance aquatic vegetation. – Oxford Science Publ.

Pirot, J. Y. 1981. Partage alimentaire et spatial des zones humides camarguaises par 5 espèces de canards en hivernage et en transit. – Paris Univ. Pierre et Marie Curie.

Pollux, B. J. A. et al. 2005. Differences in endozoochorous dispersal between aquatic plant species, with reference to plant population persistence in rivers. – Freshwater Biol. 50: 232–242.

Powers, K. D. et al. 1978. Seed distribution by waterfowl in southwestern Louisiana. – J. Wildl. Manage. 42: 598–605.

Prinzing, A. et al. 2002. Which species become aliens? – Evol. Ecol. Res. 4: 385–405.

Proctor, V. W. and Malone, C. R. 1965. Further evidence of the passive dispersal of small aquatic organisms via the intestinal tract of birds. – Ecology 46: 728–729.

Proctor, V. W. et al. 1967. Dispersal of aquatic organisms: viability of disseminules recovered from the intestinal tract of captive killdeer. – Ecology 48: 672–676.

R Development Core Team 2008. R: a language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, Austria, <www.R-project.org>.

Řehounková, K. and Prach, K. 2008. Spontaneous vegetation succession in gravel-sand pits: a potential for restoration. – Restor. Ecol. 16: 305–312.

Ridley, H. N. 1930. The dispersal of plants throughout the world. – Reeve.

Rodrigues, D. 1998. Dieta Estival e Risco de Saturnismo do Pato-real (*Anas platyrhynchos*) nos arrozais da Quinta do Canal. – Airo 9: 33–40.

Rodrigues, D. and Ferreira, M. T. 1993. Summer food and body condition of mallard (*Anas platyrhyncos* L.) in river Mondego lowlands. – Acta Vertebrata 20: 87–94.

Rodrigues, D. et al. 2002. Mallard (*Anas platyrhynchos*) summer diet in central Portugal rice-fields. – Game Wildl. Sci. 19: 55–62.

Royal Botanic Garden Edinburgh 2008. Flora Europaea. – <http://rbg-eb2.rbge.org.uk/FE/fe.html> (accessed on 9 June 2008).

Sánchez, M. I. et al. 2006. Internal transport of seeds by migratory waders in the Odiel marshes, south-west Spain: consequences for long-distance dispersal. – J. Avian Biol. 37: 201–206.

Santamaría, L. et al. 2003. Plant performance across latitude: the role of plasticity and local adpatation in an aquatic plant. – Ecology 84: 2454–2461.

Schricke, V. 1983. Distribution spatio-temporelle des populations d'anatidés en transit et en hivernage en baie du Mont Saint-Michel, en relation avec les activités humaines. – Rennes I.

Siegel, S. and Castellan, N. J. J. 1988. Nonparametric statistics for behavioural sciences, 2nd ed. – McGraw-Hill.

Soons, M. B. et al. 2008. Small seed size increases the potential for dispersal of wetland plants by ducks. – J. Ecol. 96: 619–627.

Spärck, R. 1947. Tio års viltbiologiska undersökningar i Danmark. – Svensk Jakt 85: 287–292, in Swedish.

Sterbetz, I. 1967. Economic and nature-conservation problems in feeding habits of Hungarian mallard. – Aquila 73–74: 133–145.

Street, M. 1977. The food of mallard ducklings in a wet gravel quarry, and its relation to duckling survival. – Wildfowl 28: 113–125.

Suarez, C. and Urios, V. 1999. La contaminación por saturnismo en las aves acuáticas del Parque Natural de El Hondo y su relación con los hábitos alimenticios. – Humedales Medit. 1: 83–90.

Tamisier, A. 1971. Régime alimentaire des sarcelles d'hiver *Anas crecca* L. en Camargue. – Alauda 39: 261–311, in French with English summary.

Tamisier, A. and Dehorter, O. 1999. Camargue, ducks and coots. Functioning and gradual change of a prestigious wintering ground. – Centre Ornithologique du Gard, in French.

Thomas, G. J. 1982. Autumn and winter feeding ecology of waterfowl at the Ouse Washes, England. – J. Zool. Lond. 197: 131–172.

Thuiller, W. et al. 2005. Climate change threats to plant diversity in Europe. – Proc. Nat. Acad. Sci. USA 102: 8245–8250.

Traveset, A. 1998. Effect of seed passage through vertebrate frugivores' gut on germination: a review. – Perspect. Plant Ecol. Syst. Evol. 1: 151–190.

Tutin, T. G. et al. 1964. Flora Europaea, Vol. 1. Lycopodiaceae to Platanaceae. – Cambridge Univ. Press.

Walther, G. R. et al. 2005. An ecological 'footprint' of climate change. – Proc. R. Soc. B 272: 1427–1432.

Wetlands International 2006. Waterbird population estimates, 4th ed. – Wetlands International.

Wongsriphuek, C. et al. 2008. Dispersal of wetland plant seeds by mallards: influence of gut passage on recovery, retention, and germination. – Wetlands 22: 290–299.

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