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Effect of passage through duck gut on germination of fennel pondweed seeds*

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With 1 figure and 3 tables

Abstract: Vertebrates are important seed dispersers for many plants. In addition to transport of seeds, ingestion often affects the proportion or rate of seed germination. We present one of the first studies comparing the effects of different waterbird species on the seeds of a subcosmopolitan pondweed, *Potamogeton pectinatus*. We also present the first comparison of the effects of digestion by ducks (mallard *Anas platyrhynchos*, shoveler *A. clypeata* and wigeon *A. penelope*) and physical-chemical "simulation of digestion" on pondweed seed germination. In two experiments differing in the length of the preceding stratification period, two to three individuals per duck species were force-fed 150 seeds each. Average retrieval, total germination and germination rate did not differ significantly between duck species. Germination rate was higher for duck ingested seeds, intermediate for scarified seeds (i.e. after mechanical removal of the epicarp+mesocarp) and lowest for the controls and acid treated seeds, independently of the length of the stratification period. Total germination, however, did not differ significantly among duck-ingested, scarified, control and acid treated seeds. Consequently the changes in germination rate after ingestion by ducks seem related to the grinding treatment in the gut and unrelated to exposure to acidic conditions. The coexistence of ingested and uningested seeds within a given seed cohort will increase the diversification of seed germination patterns, which can favour the colonisation of habitats characterised by unpredictable environmental conditions.

Key words: *Potamogeton pectinatus, Anas* spp., germination, dispersal, endozoochory.

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Introduction

Many species of freshwater organisms have wide geographic ranges and inhabit waterbodies that are separated by extensive terrestrial or oceanic areas (De Vlaming & Proctor 1968). This has often been interpreted as evidence that these organisms have an effective and readily available means of dispersal (Malone 1965), and birds have been considered the main candidate for dispersal (Darwin 1859, Okamura 1997).

Transport of resting stages by birds can either be external (ectozoochory) with the disseminules adhering to feathers, feet and bill or internal (endozoochory) via the digestive tract (Thienemann 1950). A number of studies have concentrated on internal transport in waterbirds and a wide variety of aquatic organisms such as algae and freshwater invertebrates (reviewed in Figuerola & Green 2002, Bilton et al. 2001) have been observed to survive passage through the digestive system of ducks.

Furthermore, it has been suggested that gut passage can trigger the germination of seeds with a thick coat and/or prolonged dormancy, such as the fruits of *Potamogeton* pondweed species (Guppy 1897, Lohammar 1954, Smits et al. 1989). A number of studies have shown that seed ingestion by birds can affect the germinability (final % germination), the rate (speed) of germination or both (e.g. Barnea et al. 1991, Traveset et al. 2001, Traveset & Verdú 2002). In the particular case of ducks, Smits et al. (1989) found that passage through the mallard *Anas platyrhynchos* gut increased seed germinability in fennel pondweed *Potamogeton pectinatus*, but not in *P. obtusifolius* and *P. natans*. However, germination rate was not monitored and no statistical comparison was attempted. Similarly, Agami & Waisel (1986) reported a significant increase in the germinability of *Najas marina* seeds following mallard gut passage: control seeds showed lower total germination than duck-ingested and mechanically cracked seeds. Germination rates of cracked and digested seeds seemed comparable, but no statistical comparison was made.

The effects of ingestion by birds can be due to the grinding effect in the gizzard, the acidic treatment in the gut or both (Charalambidou & Santamaría 2002). In most studies simulating the effects of these processes, seed germination was strongly enhanced by seed scarification (mechanical removal of the soft epicarp + mesocarp), (Crocker 1907, Lohammar 1954, Yeo 1965, Spence et al. 1971) and its combination with high temperature (Lohammar 1954), while the effect of chemical treatments was weaker (Lohammar 1954). However, Telstscherova & Hejny (1973) reported strong effects of sulphuric-acid incubation but weak effects of scarification on *P. pectinatus* seeds. To date, no study has compared the effect of gut passage on pondweed germination to the effect of the physical-chemical 'simulation of digestion' treatments. An explicit comparison between gut passage, scarification and acid-

incubation treatments may help to discern which processes (grinding in the gizzard vs. chemical treatment in the gut) govern the overall effects of ingestion by birds on seed germination.

Most of the studies mentioned above used relatively short germination runs (up to 30 days). In one of the few studies that used long germination runs (>4 weeks), seed germination continued well beyond, and often peaked after week four (LOHAMMAR 1954, with *P. pectinatus* and *P. lucens*). Hence, detected effects on total germination in previous studies may have been confounded with a short-term effect on germination rate (see TRAVESET 1998 for review).

Furthermore, most previous studies have used no or rather short periods of seed stratification previous to gut passage (or its simulation) and no stratification following it. However, LOHAMMAR's (1954) data strongly suggest that the effect of gut-passage simulation might only be evident following stratification of the treated seeds. *Potamogeton* seeds are often consumed by ducks in autumn/winter (CRAMP & SIMMONS 1977, TAMISIER & DEHORTER 1999) and seeds do not germinate until the next spring. Hence, in the field seed consumption is often both preceded and followed by several months of stratification. We thus decided to test the effect of duck digestion under prolonged stratification conditions that preceded and followed gut passage. In this study we investigated how germination rates and viability of *P. pectinatus* seeds are affected by ingestion by ducks, and how these effects are related to the mechanical and chemical components of gut passage. The effects of duck species and seed stratification are also investigated in two separate experiments.

Materials and methods

Three mallard (*A. platyrhynchos*), three wigeon (*A. penelope*) and two shoveler (*A. clypeata*) were used in our experiments. These are migratory duck species potentially capable of moving pondweed seeds over long distances (ROSE & SCOTT 1997). The mallard had been captured from the wild as adults while the widgeon and shoveler were one year-old birds born in captivity. Prior to the experiments, they were housed in outdoor facilities at Heteren, The Netherlands, and fed on a stable diet of commercial pellets (Anseres 3 ® Kasper Faunafood) and mixed grains (HAVENS Voeders) for over a year. During the experiment, they were kept individually in wooden cages (0.60 m × 0.50 m × 0.50 m) with a mesh floor (mesh size 12 mm) and removable plastic trays under each cage. The birds were caged overnight with water and pellets to familiarise them with experimental conditions. Pellets and water were available ad libitum throughout the experiments.

P. pectinatus seeds were collected in September 1998 from a population growing in an artificial lake originally created for sand-gravel extraction and situated in Engelbert (Groningen, The Netherlands). All seeds were stored in a large plastic container filled with tap water in a refrigerator (darkness, 5 ± 1 °C: stratification pre-treatment) for 7

(experiment 1) or 12 months (experiment 2). Following the experimental treatments, treated and control seeds were stored for 3 months under the same conditions (stratification post-treatment: experiments 1 and 2). We aimed at providing stratification conditions equivalent to those of Central-Northern European winters. For this purpose, and because we used mild stratification temperatures (5 °C) instead of chilling, in experiment 1 we extended the stratification for three months longer than the typical 6–7 month winter period (pre + post stratification: 10 months). Experiment 2 (pre + post stratification: 15 months) tested whether our treatment was enough to maximise total germination or whether longer stratification periods would still result in increased germination.

For the experiments, seeds were randomly assigned to the following treatments: control (kept at room temperature while the other treatments took place), duck gut passage (with 2 mallard and 2 shoveler for experiment 1, and 3 mallard and 3 wigeon for experiment 2), scarification (for experiments 1 and 2) and chemical treatment with sulphuric acid (experiment 2 only). Due to practical limitations concerning the availability of experimental animals and cages, we were not able to use the three species in both experiments. Scarification consisted in filling up triplicate 250 ml plastic flasks with seeds and wet gravel (2–4 mm grain size) and shaking them for 12 h using electric test-tube shakers. Seeds were then separated from the gravel and rinsed. Chemical treatment consisted in the immersion of triplicate batches of 50 seeds in separate test tubes containing 1 M H_2SO_4 for 5, 10, 15, 30, 60 or 120 minutes. Seeds were then thoroughly rinsed. The acid solution utilised (pH ≈ 0.3) was chosen to mimic conditions of the avian gut, which show hydrogen-acid concentrations of 0.2–1.2 for the proventriculus and 0.7–2.8 for the gizzard (Vispo & Karasov 1997). We used a relatively high acidity to facilitate comparison with Teltscherova & Hejny (1973) who treated seeds with 'concentrated sulphuric acid' for 50, 30 and 10 minutes.

Experiment 1 was carried out on 19–20 April 1999 and experiment 2 on 22–23 September 1999, i.e. at a time of the year when natural seed consumption is common (Green et al. 2002). At the beginning of each experiment, each duck was force-fed with 150 seeds (except for one individual fed with only 80 seeds, due to the accidental loss of part of the seeds during the feeding procedure). To facilitate force-feeding, groups of 20–25 seeds were placed in soft pellets made from Anseres soaked in water. The pellets were placed on the posterior part of the tongue and pushed down into the pharynx. The duck faeces were collected in the removable trays 6 and 22 hours after ingestion. Both experiments were terminated after 22 h. Immediately following collection, the faeces were sieved (sieve size 1 mm) and intact seeds were retrieved and counted. We considered seeds to be intact when they showed no visible damage to the endocarp (such as cracks in the seed wall or the opening of the seed's dorsal trap door) that resulted in exposure of the embryo. In this and other experiments (Charalambidou, unpublished data), the low proportion of 'damaged' seeds (i.e. those with broken endocarp and exposed embryo) collected always failed to germinate.

Retrieved, scarified and control seeds (experiments 1 and 2), and chemically-treated seeds (experiment 2) were then stored in tap water at 4 °C in a refrigerator for three months (stratification post-treatment, identical for experiments 1 and 2), then set to germinate in microtiter plastic trays. Each cell (3.5 ml in volume) was half-filled

with tap water (approx. 2 ml) and individual samples were placed in separate cells with a maximum of 10 seeds per cell. The trays were placed in a climate room at 15 hours light/9 hours dark at 20 °C. Germination was checked weekly and the experiments were terminated after 9 or 10 weeks (experiments 1 and 2, respectively).

Data analysis

The effect of seed treatment on total germination (cumulative germination at the end of the germination run) was tested by means of Generalised Mixed-model ANOVAs using the GLIMMIX models of SAS (SAS Institute Inc. 1996). The model included 'treatment' (gut passage vs. scarification vs. control) as a fixed effect and 'block' (i.e. each individual duck for the retrieved seeds and each replicate batch for the scarified and control seeds) as a random effect. We used a logit link for binomial data on the response variable 'proportion of germinated seeds' (number of germinated seeds/total number of seeds). When the model estimation algorithms failed to converge with this response variable, we re-expressed it as binomial data (a 0–1 variable, with one case per individual seed) to obtain a more consistent convergence (SAS Institute Inc., 1996).

We analysed experiments 1 and 2 separately. Due to the low number of individual ducks used, we split the ANOVA to increase the chance of detecting duck vs. control differences. Thus we first performed an ANOVA in which the seeds ingested by the two different duck species used were lumped in a single category ('duck ingested seeds') and compared it with the control and scarified seeds (experiments 1 and 2) and the acid-incubated seeds (experiment 2). Then in a separate ANOVA we compared the germination of duck-ingested seeds between duck species. Since these two ANOVAs were orthogonal, no Bonferroni correction was needed.

The effect of seed treatment on seed germination rate was tested by fitting a Cox proportional hazards regression model (e.g. Allison 1995) to the number of days between setting for germination and seedling emergence, for each individual seed. Cox's proportional hazards model is one of the regression techniques belonging to the broad category of 'survival analyses', used to determine the existence of significant correlations with certain independent variables when the dependent variable of interest (survival or failure time) corresponds to time until the occurrence of a particular event (in our case, germination) and it is most likely not normally distributed (since survival times usually follow an exponential or Weibull distribution). Note that each germination event is equivalent, for our purpose, to the loss of an individual in the population of non-germinated seeds. The proportional hazard model is not based on any assumptions concerning the nature or shape of the underlying survival distribution, since it models the underlying hazard rate (rather than survival time) as a function of the independent variables (Harrell 2001).

Only data from seeds that had germinated by the end of the experiment were included, to separate the effects on germination rate from those on total germination (see above). Fixed effects and specific fixed-effects contrasts were similar to those described above (see also Table 2). To account for the effects of ingestion by different individual ducks (within the 'duck' treatment), immersion in acid or scarification in dif-

Table 1. *Potamogeton pectinatus* seed retrieval following passage through the gut of different duck species. "Experiment 1" and "Experiment 2" were preceded by periods of seed stratification (storage at 5 °C) of 7 and 12 months respectively.

	Duck species	Duck individual	Number of seeds ingested	Number of seeds retrieved	% seeds retrieved
Experiment 1	Mallard	1	150	12	8
		2	80	10	12
	Shoveler	1	150	31	21
		2	150	56	37
Experiment 2	Mallard	1	150	8	5
		2	150	14	9
		3	150	0	0
	Wigeon	1	150	2	1
		2	150	44	29
		3	150	5	3

ferent batches, or germination of control seeds on different random groups, a replicate effect was added to the model as a random, or 'failtry' effect. Ties were estimated using the exact method. Survival analyses were computed using S-Plus 2000 (MathSoft 1999).

Results

Average retrieval of intact seeds was 11 % for mallard and 29 % for shoveler (experiment 1) and 5 % for mallard and 11 % for wigeon (experiment 2), with large variation among individual ducks (Table 1). The rest of seeds were digested in the ducks' digestive tract. We did not observe the regurgitation of any seed in the period that followed forced feeding (contrary to MUELLER & VAN DER VALK, 2002 who report regurgitation of wetland plant seeds in experimentally-fed mallards, but indicated that it was 'uncommon').

1. Experiment 1 (7 months pre-treatment stratification)

Seed treatment significantly affected the germination rate, but the seeds had achieved a comparable total germination at the end of the germination run (Tables 2 and 3, Fig. 1 a). Contrasts among treatments (following Bonferroni correction; experimentwise error rate, $P_{EER} = 0.05$, comparisonwise error rate, $P_{CER} = 0.017$) showed that, following gut-passage, seeds had higher germination rates than the scarified and control seeds (Table 3, Fig. 1 a). Scarified seeds had higher germination rates than control seeds (Table 3, Fig. 1 a).

Germination rate and total germination did not differ significantly between duck species (Tables 2 and 3, Fig. 1 a).

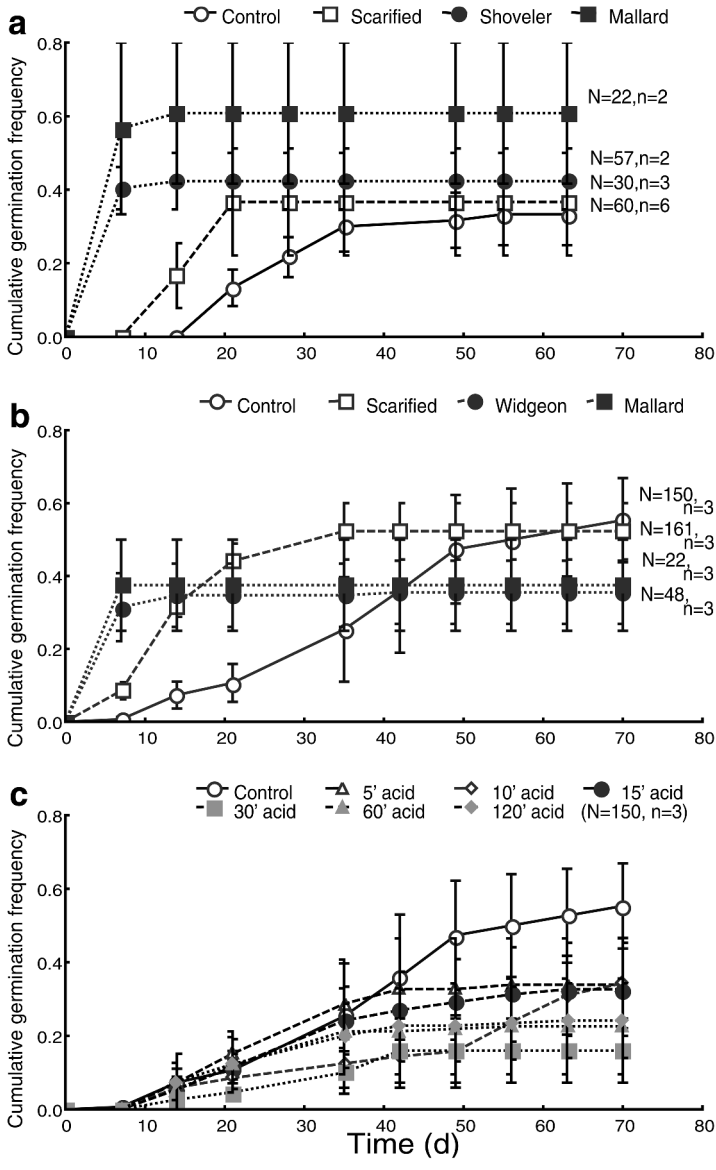

Fig. 1. Effect of experimental treatments (scarification, passage through duck gut and acid incubation) on the germination of *Potamogeton pectinatus* seeds. **(a)** Seeds stratified 7 months before and 3 months after applying the experimental treatments. **(b)** and **(c)** Seeds stratified 12 months before and 3 months after applying the experimental treatments. 'Shoveler', 'mallard' and 'wigeon' are the duck species that ingested the seeds in the gut passage treatment. '5 acid', '10 acid', etc. are the durations of seed incubation in sulphuric acid (in minutes).

Table 2. Effect of *Potamogeton pectinatus* seed treatment on total seed germination (i. e. cumulative germination at the end of the germination run, i. e. day 63 for experiment 1 and day 70 for experiment 2). Results of Generalised Mixed Models on seed germination over time. ϕ = extra-dispersion parameter. The scaled chi-square can be interpreted as a lack-of-fit statistic for the fixed component of the effect (SAS Institute Inc. 1996); hence, degrees of freedom and P-value are also provided. "df_N" and "df_D" respectively refer to the factor's and error's degrees of fredom.

	Model Statistics				Type 3 tests of fixed effects			
	ϕ	Scaled chi-square	df	P	df_N	df_D	F	P
Experiment 1								
Ducks/scarified/control	0.98	157.5	161	0.56	2	5	3.07	0.13
Mallard/Shoveler	1.01	71.3	72	0.50	1	1	1.89	0.40
Experiment 2								
Ducks/scarified/acid/control	0.94	1236	1252	0.49	8	16	1.46	0.25
Mallard/Wigeon	1.03	68.0	68	0.48	1	1	0.19	0.74

2. Experiment 2 (12 months pre-treatment stratification)

Seed treatment significantly affected the germination rate, but the seeds had achieved a comparable total germination at the end of the germination run (Tables 2 and 3; Figs. 1 b, c). Contrasts among treatments (following Bonferroni correction, as above) showed that, following gut-passage, seeds had significantly higher germination rates than the scarified, acid-incubated and control seeds (as indicated by the higher parameter estimate obtained for duck-ingested seeds in the Cox regression model, Table 3; Figs. 1 b, c). Scarified seeds had significantly higher germination rates than the acid-incubated and control seeds, which did not differ significantly (Table 3, Figs. 1 b, c).

We were not able to test for differences among acid-incubation times or for specific contrasts between each acid-incubation time and the control, because the Cox regression model failed to converge. Independently of the length of the incubation period, immersion in 1 M H_2SO_4 never stimulated seed germination. It seemed rather to have a negative effect on total germination (Fig. 1 c), although the differences among acid-incubation (all treatments pooled) and control were not significant (Tables 2 and 3).

Germination rate and total germination did not differ significantly between duck species (Tables 2 and 3, Fig. 1 b).

Discussion

Our results show that a rather small fraction of *P. pectinatus* seeds can withstand duck gut passage and germinate afterwards. Our retrieval of intact seeds

Table 3. Effect of treatment on *Potamogeton pectinatus* seed germination rate. The days to germination of each individual seed were fitted to a Cox proportional hazards regression model (MATHSOFT 1999). Parameter estimates indicate differences in the hazard rates under different treatments, relative to an arbitrarily-chosen category of reference (indicated in the table with zero values, and assigned to the "control" treatment whenever available). Increasing parameter estimates thus indicate increasing germination rates, with negative values indicating lower germination rates than the category of reference.

	χ^2	df	P	Parameter estimates ± standard error			
Experiment 1							
Duck spp. pooled				Control	Duck	Scarified	
Model fit	48.9	2	<0.0001	0	3.54±0.64	1.37±0.47	
Contrasts:							
Duck vs. control	30.9	1	<0.0001				
Duck vs. scarified	14.5	1	0.0001				
Scarified vs. control	8.55	1	0.003				
Between duck spp.				Mallard	Shoveler		
Mallard vs. shoveler	0.01	1	0.93	0	0.03±0.35		
Experiment 2							
Duck spp. pooled				Control	Duck	Scarified	Acid
Model fit	190.0	14.9	<0.0001	0	3.01±0.48	1.47±0.37	0.44±0.33
Contrasts:							
Duck vs. control	39.2	1	<0.0001				
Scarified vs. control	15.3	1	<0.0001				
Acid vs. control	1.8	1	0.18				
Duck vs scarified	10.6	1	0.001				
Duck vs. acid	40.1	1	<0.0001				
Scarified vs. acid	12.7	1	0.0004				
Between duck spp.				Mallard	Wigeon		
Mallard vs. wigeon	0.62	1	0.43	0	−0.34±0.44		

is comparable to the findings of SMITS et al. (1989; 20 % for mallard and 23 % for coot) and AGAMI & WAISEL (1986; 26 to 34 % retrieval of *N. marina* seeds ingested by mallard). We found large variation in seed retrieval among individual ducks (Table 1), despite their identical age (within each species) and diet (both within and among species). The homogeneity of environmental conditions experienced by all ducks for one year previous to the experiment (i.e. since birth for two of the species, shoveler and widgeon) points out to genotypic variation in the digestive characteristics of individual ducks as a significant source of variation in disperser quality.

In both our experiments, total cumulative germination (after 9 and 10 weeks) did not differ significantly between treatments (duck ingestion, scarification and control). Germination following gut passage or scarification was 37 to 61 %, comparable to previous work using duck-ingested seeds or simulating gut passage (CROCKER 1907, LOHAMMAR 1954, YEO 1965, SPENCE et al. 1971,

TELSTSCHEROVA & HEJNY 1973, SMITS et al. 1989). Total germination of the untreated seeds was 33 % in experiment 1 and 55 % in experiment 2, much larger than found in previous work, a difference that we attribute to the longer stratification period we used.

Germination rate, on the other hand, was significantly higher in seeds ingested by ducks and, to a lesser degree, in those with surface scarification. Even after applying large stratification periods to break seed dormancy, untreated seeds took five weeks longer to germinate (cumulative germination was comparable at day 35, Fig. 1). Thus, in climates with cold winters (temperate to sub-arctic region), gut passage will not enhance germination as opposed to seeds remaining dormant in the seed bank, but will result in an earlier germination within the same growth season. Consequently, our results support the hypothesis that duck ingestion affects the rate of germination but not the viability of the ingested seeds (see also TRAVESET 1998).

Whether an earlier germination represents fitness advantage is not self-evident: it will depend on a number of factors affecting seedling mortality and growth (advantage of an extended growth season, early mortality due to late frost or spring storms, seedling competition, etc.). It is possible, however, that the short growth seasons that characterise temperate and sub-arctic climates are the features for which early germination is most likely to represent a fitness advantage, at least in the years with mild springs. More generally, the coexistence of ingested and uningested seeds within a given seed cohort will result in increased diversification of seed germination patterns, which can favour the colonisation of habitats characterised by unpredictable climatic conditions (IZHAKI & SAFRIEL 1990).

Incubation in concentrated sulphuric acid did not result in increased total germination or higher germination rates (Fig. 1). Our results contradict the findings of TELSTSCHEROVA & HEJNY (1973) and indicate that, until more specific tests are carried out, incubation in digestive chemicals cannot be assumed to mimic duck gut passage, but suggest that the abrading of seed coats can be partially responsible for changes in germination patterns.

Passage through the gut of different duck species did not result in significant differences in seed germination. However, this result may be explained by the small number of individuals used and the fact that we did not control for retention time (time spent by each individual seed in the gut, which may have varied between species and perhaps even among individuals). In any case, our data are in agreement with a recent review by TRAVESET (1998), who concluded that interspecific differences among animals that ingest seeds have a limited effect on seed germination. Conversely, TRAVESET & VERDÚ (2002) reported differences among taxonomic groups of frugivores (birds, non-flying mammals, bats and reptiles) in their effect on seed germination.

The flyways of tens of millions of migratory ducks overlap with the global distribution of *P. pectinatus* (ROSE & SCOTT 1997), and our study shows they

have the capacity to disperse viable seeds during local movements or long-distance migrations. In this experiment, viable *P. pectinatus* seeds were retained in the duck gut for longer than 6 hours. The flying speed for *Anas* ducks ranges from 60 to 78 km/h (Welham 1994), hence waterfowl within distances of approximately 400 km may regularly disperse fennel pondweed seeds. More detailed work on the relationship between retention time in the gut and seed viability is however needed before advancing hypotheses on the spatial scale at which dispersal is likely to take place.

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