

DISPERSAL OF WETLAND PLANT SEEDS BY MALLARDS: INFLUENCE OF GUT PASSAGE ON RECOVERY, RETENTION, AND GERMINATION

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Abstract: Seed dispersal is an important process for plants, but may be particularly important for plants occurring in spatially isolated habitats like wetlands. Variation in the geographic distribution of wetland plant species may be strongly influenced by their ability to use waterbirds, particularly waterfowl to enhance dispersal. We used controlled feeding and germination experiments to investigate recovery, retention time, and germination for the seeds of 10 wetland plant species (*Chenopodium album*, *Digitaria ischaemum*, *Echinochloa colonum*, *Echinochloa crusgalli*, *Eleocharis palustris*, *Panicum dichotomiflorum*, *Polygonum lapathifolium*, *Polygonum pennsylvanicum*, *Rumex crispus*, and *Scheenoplectus maritimus*) and compared how these metrics varied with seed characteristics. We fed a known number of seeds to captive raised mallards (*Anas platyrhynchos*) and collected fecal samples every 4 hours for 48 hours; all recovered seeds were planted in seedling trays and watched for 60 days to monitor germination. We conducted 10 trials and fed each seed species in each trial, and included germination controls of non-consumed seeds. Overall, $19.0 \pm 1.8\%$ (mean \pm SE) of seeds were recovered and of recovered seeds $7.6 \pm 1.2\%$ germinated. Recovery ranged from $1.9 \pm 0.6\%$ in *D. ischaemum* to $51.0 \pm 4.7\%$ in *S. maritimus* and germination ranged from $< 0.5\%$ in *D. ischaemum* to $28.5 \pm 5.7\%$ in *R. crispus*. Recovery and germination were not related to seed size or mass ($p > 0.5$) but recovery was positively correlated with seed fiber content ($r^2 = 0.44$, $p = 0.04$). Control seeds germinated better than fed seeds for all species except *S. maritimus*, where fed seeds germinated better. Germination percentage declined with gut retention time for four of seven species. We suggest despite the large differences in viable seeds recovered, mallards may be important dispersers for the seeds of most species we studied and hypothesize that observed variation may be attributable to different plant strategies that relate to reproductive tactics and habitat type.

Key Words: *Anas platyrhynchos*, endozoochory, retention time, seed dispersal

INTRODUCTION

Seed dispersal is an important process in many ecosystems (Stapanian 1986, Herrera 1995, Campos and Ojeda 1997, Howe and Miriti 2004, McConkey and Drake 2005) that influences seed survival (Janzen 1970, Howe and Smallwood 1982, Augspurger and Kelly 1984, Howe et al. 1985, Nathan and Muller-Landau 2000), plant population genetics (Bacles et al. 2006), and plant community composition (Pollux et al. 2005). Dispersal may be particularly important for

plants occurring in spatially isolated habitats such as wetlands and riparian systems because most seeds lack the motility needed to move between basins or upstream (Ridley 1930, deVlaming and Proctor 1968, Powers et al. 1978, Pollux et al. 2005). These observations have led many authors to hypothesize that dispersal of wetland plant seeds is mediated by wetland birds, specifically waterfowl (see reviews by Charalambidou and Santamaria 2002, Figuerola and Green 2002). The association between wetland plants and waterfowl may reveal examples of directed

dispersal (e.g., Howe and Smallwood 1982, Wenny and Levey 1998, Wenny 2001).

Ducks may be especially effective dispersers of wetland seeds because they are common in wetlands, depend on wetlands throughout their annual cycle, eat wetland plant seeds, and commonly undertake long migrations between breeding, molting, and wintering areas (Heintzelman 1978, Soothill and Whitehead 1978, Todd 1996). However, compared to terrestrial systems, wetland bird-mediated dispersal has been relatively little studied (Traveset 1998, Charalambidou and Santamaria 2002, Green *et al.* 2002). Studies have found that seeds can survive intact through a duck's digestive track (Ridley 1930, deVlaming and Proctor 1968, Powers *et al.* 1978), but few have quantified seed recovery and germination rate (e.g., Mueller and van der Valk 2002, Figuerola *et al.* 2005, Pollux *et al.* 2005), and even fewer have conducted controlled experiments to provide a quantitative comparison of bird-mediated dispersal among wetland plants and compared how seed properties influence recovery, retention, and germination (Agami and Waisal 1986, Mueller and van der Valk 2002, Charalambidou *et al.* 2003, Pollux *et al.* 2005). A comparative approach may be particularly important as variation in research methodologies has made direct comparisons among studies difficult (Charalambidou and Santamaria 2002, Figuerola and Green 2002).

Developing a better quantitative understanding of ducks as dispersers of wetland plant seeds would contribute to our understanding wetland plant ecology thereby improving wetland restoration efforts (Mueller and van der Valk 2002), our ability to predict the spread of invasive exotic species (Figuerola and Green 2002), and the ability of wetland plants to respond to climate change (Davis 1989). In this study we conducted controlled feeding experiments to estimate and compare recovery frequency, retention time, and germination frequency for the seeds of different wetland plants fed to captive mallards. We compared how frequency of seed recovery and germination varied with seed characteristics (e.g., seed size), and used information on recovery and germination with information on mallard flight characteristics to estimate dispersal distances.

METHODS

Feeding Trials

Feeding trials were conducted from February 1 through April 15, 2006 at Oregon State University's Animal Science Research facility in Corvallis,

Oregon using game-farm female mallards (*Anas platyrhynchos* L.) more than five months old. When not being used in feeding trials, we confined birds in an unheated pen (4.8 m × 4.3 m × 2.5 m) where they were subject to natural temperature and photoperiod, provided with unlimited access to a commercial game bird ration (crude protein ≥ 20%, crude fat ≥ 3.0%, crude fiber ≤ 5.0%), grit, and fresh water (Petrie *et al.* 1997). Husbandry practices were approved by Oregon State University's Institutional Animal Care and Use Committee (#3328) and all individuals handling birds completed training in the ethical use of animals for research.

We justified using mallards in our experiments because they are common and widely distributed throughout the holarctic with large populations using a wide range of wetland habitats (Heintzelman 1978, Todd 1996). We fed birds the seeds of 10 common wetland plant species that are found in the diet of mallards (Drilling *et al.* 2002). Seeds were provided by Ernest Conservation Seeds (Meadville, Pennsylvania, USA) and Herbiseed, (Twyford, UK) and included Lamb's Quarters (*Chenopodium album* L.), Smooth crabgrass (*Digitaria ischaemum* (Schreber) Muhl.), Jungle rice (*Echinochloa colonum* (L.) Link.), Barnyard grass (*Echinochloa crusgalli* (L.) P. Beauv.), Common spike rush (*Eleocharis palustris* L.), Fall panicum (*Panicum dichotomiflorum* Michx.), Curltop ladysthumb (*Polygonum lapathifolium* L.), Pennsylvania smartweed (*Polygonum pennsylvanicum* L.), Curly dock (*Rumex crispus* L.), and Alkali bulrush (*Scheonoplectus maritimus* L.) (Table 1). Our study design for feeding trials was a randomized incomplete block. We divided 20 birds into two groups of 10 and conducted 10 feeding trials, alternating bird groups with each successive trial. For each trial a bird was randomly assigned a seed species and all plant species were fed during each feeding trial (n = 10 for each seed type).

Prior to each feeding trial, we weighed 1-g of seed for each species, counted the number of seeds in each sample, soaked seeds in tap water for 24 h, and then air dried each sample for 10 h (Agami and Waisal 1986, Mueller and van der Valk 2002). We controlled for mass because previous work has indicated passage rates may vary with meal size (Clark and Gentle 1990). To control the number of seeds ingested during each feeding trial, we precision-fed each bird by inserting a tube (1.2 cm × 40 cm) into the esophagus and carefully poured the seeds into the tube using a funnel. We then gently pushed the seeds down through the tube with a wooden dowel (Dugger *et al.* 2007). We subtracted any regurgitated seeds and seeds that stuck to the inside of the tube during feeding from the total

Table 1. Select characteristics for the seeds of 10 wetland plant species fed to captive raised female mallards.

Common name	Scientific name	Family	NDF (%) ¹	Seed Type	Seed mass ² (mg)	Seed size ³ (mm)
Lamb's quarter	<i>Chenopodium album</i>	Chenopodiaceae	27	Utricle	0.69 ± 0.02	1.40 × 1.33
Smooth crabgrass	<i>Digitaria ischaemum</i>	Poaceae	26.6	Caryopsis	0.49 ± 0.02	2.03 × 0.98
Jungle rice	<i>Echinochloa colonum</i>	Poaceae	22.1	Caryopsis	1.44 ± 0.03	2.46 × 1.51
Barnyard grass	<i>Echinochloa crusgalli</i>	Poaceae	19.5	Caryopsis	3.28 ± 0.06	4.09 × 1.80
Common spikerush	<i>Eleocharis palustris</i>	Cyperaceae	47.9	Achene	0.57 ± 0.02	1.51 × 1.07
Fall panicum	<i>Panicum dichotomiflorum</i>	Poaceae	32.2	Caryopsis	0.47 ± 0.02	1.72 × 0.89
Curltop ladysthumb	<i>Polygonum lapathifolium</i>	Polygonaceae	30.2	Achene	2.34 ± 0.05	2.48 × 2.08
Pennsylvania smartweed	<i>Polygonum pennsylvanicum</i>	Polygonaceae	29.8	Achene	6.16 ± 0.10	3.15 × 2.68
Curly dock	<i>Rumex crispus</i>	Polygonaceae	11.4	Achene	1.51 ± 0.03	2.13 × 1.38
Alkali bulrush	<i>Scheuchzeria maritima</i>	Cyperaceae	39.2	Achene	3.08 ± 0.05	3.29 × 2.17

¹ NDF indicates neutral detergent fiber.

² mean ± SE.

³ values present means from measuring 30 seeds.

number of seeds; thus, we knew the exact number of seeds fed to each experimental bird. All trials started at 0800. After feeding, we placed each duck in a 20 cm × 20 cm × 30 cm cage where they remained, provided with water *ad libitum*, throughout the trial (48 h). We did not feed birds during the trial, simulating fasting during migration (e.g., Figuerola and Green 2005). We placed metal funnels under each chamber that directed fecal matter into a plastic bag (Dugger et al. 2007). We collected the bird excreta (replaced the bags below each cage) every 4 hours for 48 hours (n = 12 samples/bird/trial) and refrigerated each bag at 4°C until processing. In the lab, we rinsed each fecal sample through a 250 µm sieve with tap water, and removed and counted all intact seeds retained by the screen. Seeds were then air dried for 12 h and placed in individually labeled envelopes. We stored each 4-h sample separately in paper bags in the refrigerator at 4°C for one month until germination trials began (Charalambidou et al. 2003, Pollux et al 2005).

Spring Planting Protocol

To estimate viability of ingested seeds and compare viability between ingested and uningested (control) seeds, we planted retrieved seeds and control seeds in germination trays (Powers et al. 1978, Agami and Waisel 1986, Figuerola et al. 2002, Charalambidou et al. 2003) filled with horticulture mixture soil (SUN GRO Mix A w/DE, Horticulture Department, Oregon State University, USA). We created control samples of 100 seed of each plant and treated controls to the same preparation (e.g.,

soaking with tap water, drying, and refrigeration) and germination conditions as retrieved seeds. Retrieved seeds from each trial, bird, and sample period (4, 8,..., 48 hours) were planted in separate cells (2.5 cm × 2.5 cm in size) in the germination tray with up to 5 seeds planted in each cell. We watered seeds daily and rotated germination trays on the bench to reduce the effect of bench position on seed germination. We defined seed germination as the emergence of the cotyledon and checked germination every 3 days for 60 days, removing germinated seeds as they were detected to avoid recounting (Shipley and Parent 1991, Charalambidou et al. 2005).

Data Analysis and Predictions

Based on previous published work and our personal observations from previous feeding experiments, we predicted recovery and germination rates would differ among seeds. Specifically we predicted that recovery would be higher for smaller seeds (deVlaming and Proctor 1968) and for seeds with tougher seed coats (deVlaming and Proctor 1968, Mueller and van der Valk 2002), that most seed would be retrieved within 24 hours of feeding, and that the number of seeds retrieved would decrease considerably thereafter (Mueller and van der Valk 2002, Charalambidou et al. 2003, Pollux et al. 2005). We further predicted that germination frequency would decline with retention time because seeds subjected to longer digestion are less likely to survive (Charalambidou et al. 2003).

We first tested for differences in total intact seed recovered and germinated using mixed general linear

Table 2. Retrieval and germination characteristics for the seeds of 10 wetland plant seeds ingested by mallards.

Species	Ingested Seeds ($\bar{x} \pm SE$)	% Retrieved Seeds ¹ ($\bar{x} \pm SE$)	% Germinated Seeds ² ($\bar{x} \pm SE$)	% Viable ³	Maximum RT(h) ⁴	
					R	G
<i>Chenopodium album</i>	1,425.3 \pm 41.5	9.8 \pm 2.4b [†]	12.9 \pm 4.2bc	1.3	48	0
<i>Digitaria ischaemum</i>	2,083.7 \pm 58.6	1.9 \pm 0.6a	0.0a	0.0	24	16
<i>Echinochloa colonum</i>	783.8 \pm 6.4	8.5 \pm 1.7b	8.6 \pm 4.3bce	0.7	24	16
<i>Echinochloa crusgalli</i>	332.3 \pm 33.2	10.7 \pm 3.7b	5.7 \pm 1.7bc	0.6	32	4
<i>Eleocharis palustris</i>	1,964.4 \pm 46.1	39.9 \pm 4.7cd	0.1 \pm 0.0a	0.0	48	24
<i>Panicum dichotomiflorum</i>	2,153.3 \pm 59.9	12.8 \pm 3.7b	8.4 \pm 2.7bc	1.1	44	36
<i>Polygonum lapathifolium</i>	514.8 \pm 24.9	16.0 \pm 3.6bc	4.7 \pm 1.5bc	0.7	44	16
<i>Polygonum pennsylvanicum</i>	237.3 \pm 8.2	21.3 \pm 2.7bcd	0.4 \pm 0.2ae	0.1	48	0
<i>Rumex crispus</i>	740.3 \pm 8.3	18.6 \pm 3.2bc	28.5 \pm 5.7cd	5.3	48	24
<i>Scheonoplectus maritimus</i>	391.1 \pm 6.2	51.1 \pm 4.7d	7.1 \pm 1.4b	3.6	48	28

[†] values with the same letter in each column are not significantly different.

¹ % Retrieved Seeds = (number of seeds retrieved/number of seeds fed) \times 100.

² % Germinated Seed = (number of seed retrieved that germinated/number of seeds retrieved) \times 100.

³ % Viable seed recovered = (mean % of seed recovered * mean % of seeds germinated) \times 100.

⁴ Maximum RT = maximum retention time of retrieved (R) and germinated (G) seeds.

models (PROC MIXED, v. 9.1, SAS Institute 2005; Littell *et al.* 2002). The response variable, either total proportion of fed seeds recovered or total proportion of fed seeds that germinated, was first $\log(x + 0.05)$ transformed, which normalized the residuals and adjusted for zeros in the data set. Explanatory variables included plant species (fixed effect) and bird group (random effect). We used Type III sums of squares when interpreting results, and a Tukey multiple comparison procedure to test among pairs of least-squared predicted means using an experimentwise error rate of 0.10. In a separate mixed model analysis, we tested for the influence of time since feeding on recovery and germination frequency using percent recovered seed and percent germinated seed (transformed as above) as the response variable, time (4 hour blocks over a 48 hour period), plant species, and their interaction as explanatory variables, and bird group as a random effect. The overall model indicated there was a species by time period interaction for both recovered ($F_{99,1200} = 1.5$, $p = 0.002$) and germinated seed ($F_{99,1200} = 2.5$, $p < 0.0001$), so we conducted analyses for the influence of time separately for each species.

Next, we used linear regression to test for relationships between seed characteristics (seed size, seed mass, and seed coat toughness) and the proportion of total retrieved and germinated seeds. We measured and weighed 30 seeds of each species and used the mean value as our estimate of size and mass in the analysis (Table 1). We used percent

neutral detergent fiber (NDF) in the seed as a measure of seed toughness. NDF, estimated using the Ankom A200 filter bag technique (calculated from two 1-g seed samples; AOAC 2000), is a measure of non-digestible hemi-cellulose, cellulose, and lignin cell constituents that influence seed coat strength. We determined if germination of fed seeds differed from control seeds by calculating the mean and 95% confidence limits for fed seeds from our 10 trials and comparing our estimate of germination for controlled seeds against those confidence limits. Finally, to understand how far viable seeds might be dispersed across the landscape, we converted our time intervals to distance traveled by multiplying each time interval by 90 km h⁻¹, an empirical estimate of mallard flight speed during migration (Bellrose and Crompton 1981).

RESULTS

Overall, the mean percentage of intact seed retrieved was 19.0 \pm 1.8% ($n = 100$). Percentage retrieved did not vary by bird group ($F_{1,100} = 3.9$, $p > 0.10$) but differed significantly among plant species ($F_{9,100} = 13.9$, $p < 0.0001$), ranging from 1.9 \pm 0.6% for *D. ischaemum* to 51.0 \pm 4.7% for *S. maritimus* (Table 2). There was no difference in recovery between the two pairs of congeneric species (*Echinochloa crusgalli* v. *E. colonum*; *Polygonum lapathifolium* v. *P. pennsylvanicum*) fed during the trial (all p -values > 0.20). Percentage of seed retrieved

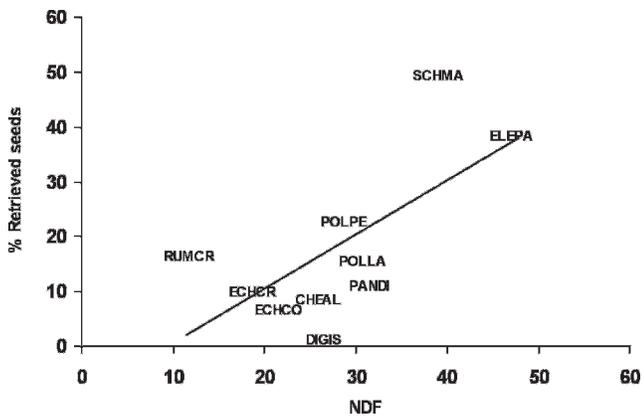


Figure 1. Relationship between the mean percent seed retrieved for each trial and seed neutral detergent fiber (NDF) for the seeds of 10 species of wetland plants fed to captive raised mallards.

was not related to seed mass ($p = 0.82$) or seed size ($p = 0.63$) but it was positively related to neutral detergent fiber ($r^2 = 0.44$, $p = 0.037$; Figure 1). The largest percentage of seeds was recovered during the first 4 hour time period for all species and varied from $46.0 \pm 7.4\%$ for *E. palustris* to $82.0 \pm 5.6\%$ for *R. crispus* (Figure 2). While retrieval frequency declined with time for all species (all p -values < 0.001), the species by time interaction ($F_{11,1200} = 1.38$, $p = 0.01$) indicated that the rate of attenuation varied among species.

The mean percentage of recovered seed that germinated was $7.6 \pm 1.2\%$ (range 0–28.5%) and was similar between bird groups ($F_{1,100} = 0.1$, $p = 0.76$), but differed by plant species ($F_{9,100} = 11.1$, $p < 0.001$; Table 2). Proportion germinated did not vary with seed size ($p = 0.93$) or seed mass ($p = 0.51$), but decreased with increasing NDF ($p = 0.04$). Germination frequency was highest for *R. crispus* ($28.5 \pm 5.7\%$) and lowest for *D. ischaemum*, *P. pensylvanicum*, and *E. palustris* ($< 0.5\%$). There was no correlation between the proportion of seeds retrieved and the proportion of seeds that germinated ($p = 0.24$). Germination of control seeds compared to fed seeds was higher for eight species; similar for *P. pensylvanicum*, and lower for *S. maritimus* (Figure 3).

Because seed recovery was skewed across time periods (Figure 2), our ability to test how retention time influenced germination was constrained by zeros in the data set at the longer time intervals. We tested for a time influence using only those time intervals for each species where at least five trials resulted in recovered seeds (4–28 h for *S. maritimus*; 4–12 h for *P. dichotomiflorum*, *P. lapathifolium*, and *R. crispus*; and 4–8 h for *C. album*, *E. crusgalli*, and *E. colonum*). Because of low recovery and overall low germination frequency, we could not test for a

time effect on *D. ischaemum*, *E. palustris*, or *P. pensylvanicum*. As the number of intervals varied across species, we conducted the analysis separately for each species. Germination frequency varied by time for *E. crusgalli* ($F_{1,18} = 1.9$, $p = 0.03$), *P. lapathifolium* ($F_{2,27} = 8.9$, $p = 0.03$), *R. crispus* ($F_{2,27} = 6.8$, $p = 0.03$), and *S. maritimus* ($F_{6,63} = 2.9$, $p = 0.01$) but not for *P. dichotomiflorum* ($p = 0.06$), *E. colonum* ($p = 0.18$), or *C. album* ($p = 0.20$). Germination was higher for seeds collected at 4 hours vs. those collected at 8 h for *E. crusgalli*, higher for seeds collected at 4 h vs. 8 h and 12 h for *P. lapathifolium*, and *R. crispus*, and higher for seeds collected at 4 h vs. 28 h for *S. maritimus*. All other paired comparisons were similar (Table 3).

The percentage of all seeds fed that were excreted and germinated ranged from 0.0–5.3% (Table 2). We estimated a potential dispersal distance for *C. album*, *P. dichotomiflorum*, *R. crispus*, and *S. maritimus*, the four species with the greatest number of germinated seeds. Viable seeds for all species could be carried up to 720 km, with the seed of *S. maritimus* potentially being carried over 2,000 km (Table 4).

DISCUSSION

At least some seed of all but one species, *Digitaria ischaemum*, successfully germinated after passage through the mallard gut. However, the considerable difference in recovery frequency and germination suggests the ability of mallards to disperse wetland plant seeds varies considerably. Among seed eating ducks, mallards have relatively well developed gizzards, and gizzard size has been correlated with recovery frequency (Charalambidou and Santamaría 2002, Figuerola et al. 2002). Additional work using other duck species will likely reveal important heterogeneity in dispersal capabilities by ducks (e.g., Charalambidou et al. 2003) that will have important implications for wetland plant dispersal.

We did not keep track of individual birds during our feeding experiments (although that was our initial intent). Because of this oversight, some birds may have been fed a species of seed more than once and we could not control for individual variation among birds in our analysis. This oversight likely resulted in some pseudoreplication, which can influence results, particularly if individual birds varied considerably in their digestive performance (Figuerola and Green 2002). Our experimental birds were captive raised, the same age, and they came from the same facility so they experienced similar diets and housing conditions prior to and during our study. This should have helped minimize individual variation. In fact we found no difference among

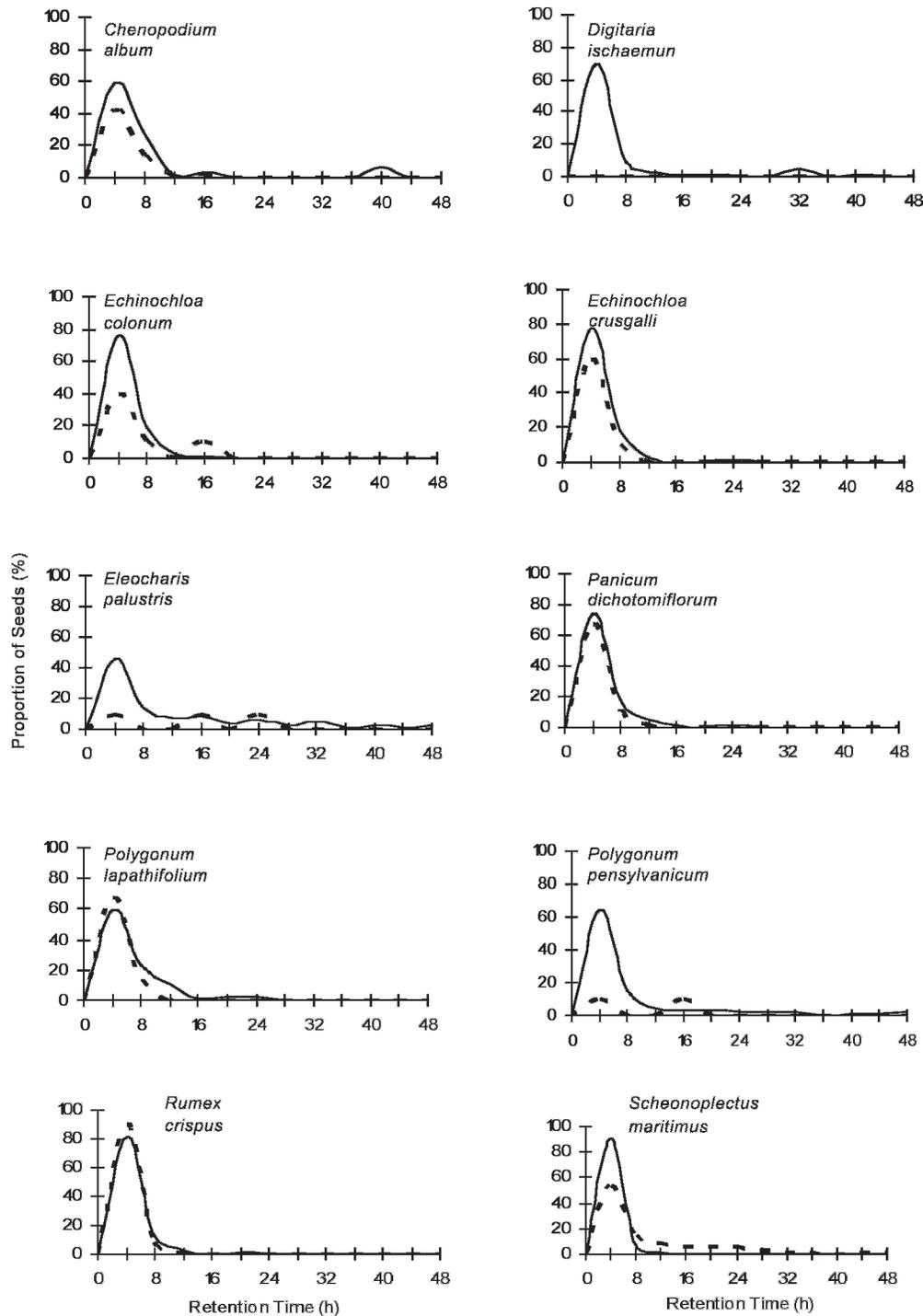


Figure 2. Percentage of seed retrieved (solid line) and germinated (dashed line) by time after feeding (seeds collected at 4 hour intervals) for the seeds of 10 species of wetland plants fed to captive raised mallards. Most seed was retrieved within 24 hours.

experimental groups, but we repeat a previous recommendation that all future studies control for individual variation in their analyses (Figuerola and Green 2002).

Similar to previous studies, most seeds were recovered fairly quickly following feeding and

frequency declined thereafter with almost all seeds recovered within 24 hours. However, at least some seed was recovered out to 48 hours suggesting that, while rare, very long distance dispersal may occasionally occur (deVlaming and Proctor 1968). Recovery frequency was higher for seeds with a

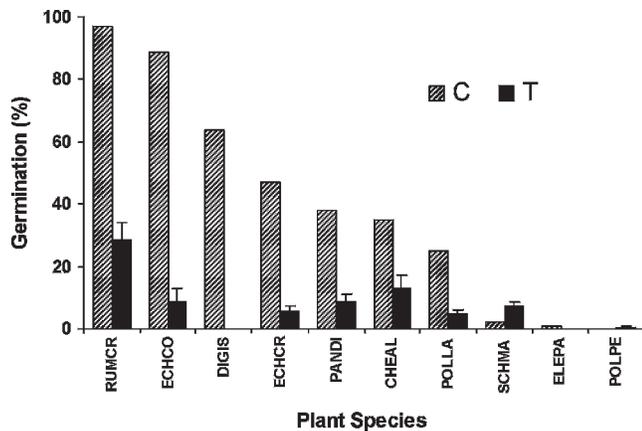


Figure 3. A comparison of germination rate for unfed seeds (control) vs. seeds fed and recovered from the digestive tract of mallards (treatment; mean \pm SE) for 10 wetland plant species (*Chenopodium album*, CHEAL; *Digitaria ischaemum*, DIGIS; *Echinochloa colonum*, ECHCO; *Echinochloa crusgalli*, ECHCR; *Eleocharis palustris*, ELEPA; *Panicum dichotomiflorum*, PANDI; *Polygonum lapathifolium*, POLLA; *Polygonum pensylvanicum*, POLPE; *Rumex crispus*, RUMCR; *Scheonoplectus maritimus*, SCHMA).

higher fiber content (our surrogate measure of seed coat toughness), but even for those species prolonged retention reduced survival. Many studies infer that seed coat strength is an important quality influencing survival for wetland plant seeds; however, most have relied on indirect measures of seed coat toughness (deVlaming and Proctor 1968, Mueller and van der Valk 2002, this study). There are methods for directly measuring seed hardness, and given most studies have found this an important factor influencing seed survival, we recommend a direct measure of seed hardness be universally adopted to allow quick and objective comparison among seeds of many plant species and among studies.

Contrary to our predictions and other studies (deVlaming and Proctor 1968, Mueller and van der

Valk 2002), we found no relationship between recovery and seed size while germination was inversely related to NDF. It is possible such differences result from variation in characteristics of our experimental birds. Mallard gut morphology varies with diet (Miller 1975); the extent this variation can influence seed retention and digestive efficiency, which might contribute to differences between studies, is unknown. In one study, diet was associated with recovery frequency but not retention time (Charalambidou et al. 2005). Alternately, discrepancies among studies may reflect differences in methodologies or other sources of variation in seeds or birds that can make direct comparisons among studies difficult (Figuerola and Green 2002). For example, as a comparison, we fed two species that were also fed in a previous study (Mueller and van der Valk (2002). In one case (*C. album*), the percent seed recovered was similar (13.2% v. 9.8%), but in the second (*E. crusgalli*), our recovery was considerably higher (10.7% vs. 1.9%). The reason for this difference is unclear; both studies used captive raised birds that were precision fed in controlled experiments, and both studies fed some combination of commercial duck chow and grit between experiments. Mueller and van der Valk (2002) provided birds access to food during their experiments, while we fasted our birds. Recent work has indicated that fasting can influence survival and retention time (Figuerola and Green 2005), but more work is needed to quantify these relationships. Our estimates of germination for *E. crusgalli* (5.7%) and *C. album* (13.9%) were considerably lower than viability estimated using tetrazolium (53.4% and 24.1%) in Mueller and van der Valk (2002). Our estimates of germination are likely conservative because we exposed all seeds to a relatively homogenous set of germination conditions. However, simple viability tests overestimate germination frequency because not all viable seeds germinate. Given the differences,

Table 3. Mean germination percentage (SE) of wetland plant seeds fed to mallards (n = 10 trials per species) by gut retention time.

Species	Gut Retention Time ¹ (hr)						
	4	8	12	16	20	24	28
<i>Chenopodium album</i> ²	13.9 (7.6)a	7.6(4.0)a
<i>Echinochloa colonum</i>	5.9(4.2)a	2.9(2.9)a
<i>Echinochloa crusgalli</i>	9.8(4.8)a	5.0(5.0)b
<i>Panicum dichotomiflorum</i>	7.0(3.8)a	2.3(1.9)a	3.3(3.3)a
<i>Polygonum lapathifolium</i>	4.8(1.9)a	2.0(1.5)b	0.0b
<i>Rumex crispus</i>	32.0(6.7)a	11.7(5.2)b	17.4(11.3)b
<i>Scheonoplectus maritimus</i>	6.2(1.2)a	5.4(2.9)a	6.7(3.7)a	5.1(2.3)a	4.1(2.2)a	4.3(2.3)a	1.1(1.1)b

¹Time = collection hour post feeding; measure of gut retention time.

²Values in each row with different letters are statistically different.

Table 4. The percent of viable seed that could be dispersed varying distances (360–2,520 km) based on recovery rate, germination rate and mallard flight speed during migration (90 km h⁻¹).

Species	Potential Dispersal Distance (km)						
	0–360 ¹	720	1,080	1,440	1,800	2,160	2,520
<i>Chenopodium album</i>	1.73	1.09	0.01	0.19	0.00	0.00	0.00
<i>Panicum dichotomiflorum</i>	1.00	0.72	0.00	0.00	0.00	0.00	0.00
<i>Rumex crispus</i>	4.29	0.30	0.07	0.00	0.00	0.00	0.00
<i>Scheonoplectus maritimus</i>	0.87	1.06	0.12	0.09	0.24	0.12	0.01

¹ The value in each cell represents the proportion of ingested seed that was excreted during each four hour time block. Potential dispersal distance was calculated by multiplying each time interval (4, 8, 12, 16, 20, 24, 28h) by mallard flight speed.

care should be taken to select a method most appropriate for the question. Because gut passage can influence seed response in ways more subtle than a simple live/die dichotomous response (Espinar *et al.* 2004, Pollux *et al.* 2005), we recommend continued use of germination experiments.

Our analysis of germination with retention time was hampered because of low seed recovery during many time intervals, but germination declined with time in four of seven species tested, and all species showed some evidence for declining germination with time. The largest drop in germination was between the four and eight hour time intervals, but additional data for germination at longer intervals are needed to discern patterns. Germination was most consistent across time for *S. maritimus* where germination was similar for seeds collected up to 24 hours. Few studies have quantified how germination changes with retention time, but our results are consistent with a study of *Ruppia maritima* (Charalambidou *et al.* 2003) and *Sparganium emersum* and *Sagittaria sagittifolia* (Pollux *et al.* 2005). In the case of *R. maritima*, the trend held across several species of dabbling duck (*Anas* spp.).

A recent review suggested the circumstances required for ducks to be effective long distance seed dispersers (> 300 km) may rarely develop (Clausen *et al.* 2002). However, considering the large number of seeds consumed by ducks each year, we suggest that duck-mediated dispersal is likely an important mechanism for many wetland plant species. For example, using our data on seed mass and viable recovery rate for *E. crusgalli* (Tables 1 and 2) and data on *E. crusgalli* production and consumption by ducks in a managed wetland in the Midwestern United States (Greer *et al.* 2007), we estimate that 1,028,463 viable seeds/ha would be excreted by ducks. If only one for every 1,000–100,000 is successful, 10–1,000 successful dispersal events originate from every hectare of wetland. Even if dispersal of several hundred kilometers is rare, it may be sufficient to maintain genetic connectivity, and regional movements of 25–50 km may be

important for population persistence, particularly in freshwater systems where wetland abundance and distribution vary considerably among years.

Most examples of bird-mediated dispersal come from terrestrial systems where plants have evolved brightly colored fruits that advertise their seeds and provide nutritional benefits to dispersers (Traveset 1998). Mallards (along with most seed eating ducks) are primarily tactile feeders, filtering unseen seeds from the bottom of wetlands; consequently, brightly colored fruits would be of little value to plants seeking to attract ducks as dispersers. Are there other characteristics of the seeds we fed that suggest an adaptation for bird-mediated dispersal? For species like *D. ischaemum*, where no seeds survived gut passage, mallards are clearly only seed predators. At the other extreme, *S. maritimus* produces hard seeds that are excreted at a high rate, germination is constant for seeds retained up to 24 h, and germination of fed seeds is higher than controls, a pattern seen in many terrestrial plants that use birds to disperse their seeds (Traveset 1998) as well as a few wetland plants (Agami and Waisel 1986, Pollux *et al.* 2005).

For all but *S. maritimus*, control seeds germinated better than fed seeds, suggesting ducks function primarily as seed predators. However, we hypothesize the variation in recovery and germination among species reflects differences in the relative importance of ducks as dispersers and different evolutionary strategies for using ducks as dispersers, with optimal strategies being influenced by habitat conditions and the role seeds play in the life-history of each plant. For example, *Scheonoplectus maritimus* occupies more predictable wetland habitats where the encounter rate with ducks is high each year. *S. maritimus* produces a relatively small number of hard to digest seeds that survive in high proportion when consumed, are retained for longer periods, and maintain viability longer. The same traits that increase seed survival when consumed make the seeds less nutritious to ducks (Petrie *et al.* 1997, Dugger *et al.* 2007). This combination of traits

maximizes seed survival when consumed and increases the distance that viable seeds can be transported, possibly at the expense of attracting bird dispersers (e.g., Miller 1987). *S. maritimus* relies heavily on vegetative reproduction, thus seeds may be most important for long-distance dispersal or survival during prolonged periods of drought. In contrast, species like *E. crusgalli* and *R. crispus* produce a large number of seeds that are nutritious to ducks; these seeds have a lower overall survival rate when consumed and steeper mortality curve with gut retention time. Although the proportion of seeds that survive transit through the mallard gut is small compared to *S. maritimus*, the total number consumed and excreted is still large. Species like *R. crispus* rely solely on seeds for yearly production and occupy more ephemeral wetlands whose size and distribution vary considerably in space and time. Thus, they may sacrifice a percentage of their reproductive effort each year to attract ducks and increase the number of dispersal events, increasing the likelihood of some seed being dispersed to suitable sites. Consistent with this explanation *R. crispus* turns a distinctive red-brown color in fall that contrasts with the straw coloring of most wetland plants, which could serve to advertise the location of its seeds. The steeper decline in seed survival with retention time for species like *R. crispus* and *E. crusgalli* suggests long distance transport may be less frequent than for *S. maritimus*.

From a management perspective, the consequences of understanding dispersal have been discussed relative to wetland restoration (Mueller and van der Valk 2002) and more recently wetland conservation policy (Amezaga et al. 2002). Additional work is needed to investigate the role of ducks in dispersing the seeds of exotic species. Less understood and possibly more subtle, wetland managers may influence the seed pool available to be dispersed by ducks by managing habitats to favor a few species. Refuges concentrate large numbers of ducks that move between refuges and the surrounding landscape, which may have consequences for regional wetland plant community composition.

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LITERATURE CITED

- Agami, M. and Y. Waisel. 1986. The role of mallard ducks (*Anas platyrhynchos*) in distribution and germination of seeds of the submerged hydrophyte *Najas marina* L. *Oecologia* 68:473–75.
- Amezaga, J. M., L. Santamaría, and A. J. Green. 2002. Biotic wetland connectivity—supporting a new approach for wetland policy. *Acta Oecologica* 23:213–22.
- Association of Official Analytical Chemists (AOAC). 2000. Official Methods of Analysis, seventeenth edition. Association of Analytical Chemists, Washington DC, USA.
- Augsburger, C. K. and C. K. Kelly. 1984. Pathogen mortality of tropical tree seedling: experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia* 61:211–17.
- Bacles, C. F. E., A. J. Lowe, and R. A. Ennos. 2006. Effective seed dispersal across a fragmented landscape. *Science* 311:628.
- Bellrose, F. C. and R. C. Crompton. 1981. Migration speeds of three waterfowl species. *Wilson Bulletin* 93:121–24.
- Campos, C. M. and R. A. Ojeda. 1997. Dispersal and germination of *Prosopis flexuosa* (Fabaceae) seeds by desert mammals in Argentina. *Journal of Arid Environments* 35:707–14.
- Charalambidou, I. and L. Santamaría. 2002. Waterbirds as endozoochorous dispersers of aquatic organisms: a review of experimental evidence. *Acta Oecologica* 23:165–76.
- Charalambidou, I., L. Santamaría, C. Jansen, and B. A. Nolet. 2005. Digestive plasticity in mallard ducks modulates dispersal probabilities of aquatic plants and crustaceans. *Functional Ecology* 19:513–19.
- Charalambidou, I., L. Santamaría, and O. Langevoord. 2003. Effect of ingestion by five avian dispersers on the retention time, retrieval and germination of *Ruppia maritima* seeds. *Functional Ecology* 17:747–53.
- Clark, R. G. and G. C. Gentle. 1990. Estimates of grain passage time in captive mallards. *Canadian Journal of Zoology* 68:2275–79.
- Clausen, P., B. A. Nolet, A. D. Fox, and M. Klaassen. 2002. Long-distance endozoochorous dispersal of submerged macrophyte seeds by migratory waterbirds in northern Europe – a critical review of possibilities and limitations. *Acta Oecologica* 23:191–203.
- Davis, M. B. 1989. Lags in vegetation response to greenhouse warming. *Climatic Change* 15:75–82.
- deVlaming, V. and V. W. Proctor. 1968. Dispersal of aquatic organisms: viability of seeds recovered from the droppings of captive killdeer and mallard ducks. *American Journal of Botany* 55:20–26.
- Drilling, N., R. Titman, and F. McKinney. 2002. Mallard (*Anas platyrhynchos*). In A. Poole and F. Gill (eds.) *The Birds of North America*, No. 658. The Birds of North America, Inc., Philadelphia, PA, USA.
- Dugger, B. D., M. L. Moore, R. S. Finger, and M. J. Petrie. 2007. True metabolizable energy for seeds of common moist-soil plant species. *Journal of Wildlife Management* 71:1964–67.
- Espinar, J. L., L. V. Garcia, J. Figuerola, A. J. Green, and L. Clemente. 2004. Helophyte germination in a Mediterranean salt marsh: gut passage by ducks changes seed response to salinity. *Journal of Vegetation Science* 15:315–22.
- Figuerola, J. and A. J. Green. 2002. Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. *Freshwater Biology* 47:483–94.
- Figuerola, J. and A. J. Green. 2005. Effects of premigratory fasting on the potential for long distance dispersal of seeds by waterfowl: an experiment with marbled teal. *Revue D Ecologie-La Terre Et La Vie* 60:283–87.
- Figuerola, J., A. J. Green, and L. Santamaría. 2002. Comparative dispersal effectiveness of wigeon grass seeds by waterfowl wintering in south-west Spain: quantitative and qualitative aspects. *Journal of Ecology* 90:989–1001.
- Figuerola, J., L. Santamaría, A. J. Green, I. Luque, R. Alvarez, and I. Charalambidou. 2005. Endozoochorous dispersal of aquatic plants: does seed gut passage affect plant performance? *American Journal of Botany* 92:696–99.

- Green, A. J., J. Figuerola, and M. I. Sánchez. 2002. Implications of waterbird ecology for the dispersal of aquatic organisms. *Acta Oecologica* 23:177–89.
- Greer, A. K., B. D. Dugger, D. A. Graber, and M. J. Petrie. 2007. The effects of seasonal flooding on seed availability for spring migrating waterfowl. *Journal of Wildlife Management* 71:1561–66.
- Heintzelman, D. S. 1978. *North American Ducks, Geese, and Swans*. Winchester Press, New York, NY, USA.
- Herrera, M. C. 1995. Plant-vertebrate seed dispersal system in the Mediterranean: ecology, evolutionary, and historical determinants. *Annual Review of Ecology and Systematics* 26:705–27.
- Howe, H. F. and M. N. Miriti. 2004. When seed dispersal matters. *BioScience* 54:651–60.
- Howe, H. F., E. W. Schupp, and L. C. Westley. 1985. Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). *Ecology* 66:781–91.
- Howe, H. H. and J. Smallwood. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13:201–28.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104:501–28.
- Littell, R. C., W. W. Stroup, and R. J. Freund. 2002. *SAS for Linear Models*, fourth edition. SAS Institute Inc., Cary, NC, USA.
- McConkey, K. R. and R. D. Drake. 2005. Flying foxes cease to function as seed dispersers long before they become rare. *Ecology* 87:271–76.
- Miller, M. R. 1975. Gut morphology of mallards in relation to diet quality. *Journal of Wildlife Management* 39:168–73.
- Miller, M. R. 1987. Fall and winter foods of northern pintails in the Sacramento Valley, California. *Journal of Wildlife Management* 51:405–14.
- Mueller, M. H. and A. G. van der Valk. 2002. The potential role of ducks in wetland seed dispersal. *Wetlands* 22:170–78.
- Nathan, R. and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution* 15:278–84.
- Petrie, M. J., R. D. Drobney, and D. A. Graber. 1997. Evaluation of true metabolizable energy for waterfowl. *Journal of Wildlife Management* 61:420–25.
- Pollux, B. J., A. L. Santamaria, and N. J. Ouborg. 2005. Differences in endozoochorous dispersal between aquatic plant species, with reference to plant population persistence in rivers. *Freshwater Biology* 50:232–42.
- Powers, K. D., R. E. Noble, and R. H. Chabreck. 1978. Seed distribution by waterfowl in southwestern Louisiana. *Journal of Wildlife Management* 42:598–605.
- Ridley, H. N. 1930. *The Dispersal of Plants Throughout the World*. L. Reeve & Co. Ltd., Ashford, Kent, UK.
- Shipley, B. and M. Parent. 1991. Germination responses of 64 wetland species in relation to seed size, minimum time to reproduction and seeding relative growth rate. *Functional Ecology* 5:111–18.
- Soothill, E. and P. Whitehead. 1978. *Wildfowl of the World*. Blandford Press, Poole, UK.
- Stapanian, M. A. 1986. Seed dispersal by birds and squirrels in the deciduous forests of the United States. p. 325–36. *In* A. Estrada and T. H. Fleming (eds.) *Frugivores and Seed Dispersal*. W. Junk Publishers, The Hague, Netherlands.
- Todd, F. S. 1996. *Natural History of the Waterfowl*. Ibis Publishing Co., San Diego, CA, USA.
- Traveset, A. 1998. Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspectives in Plant Ecology, Evolution and Systematics* 1:151–90.
- Wenny, D. G. 2001. Advantages of seed dispersal: a re-evaluation of directed dispersal. *Evolutionary Ecology Research* 3:51–74.
- Wenny, D. G. and D. J. Levey. 1998. Directed seed dispersal by bellbirds in tropical cloud forest. *Proceedings of the National Academy of Science* 95:6204–07.

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