

1 **Plant dispersal by teal (*Anas crecca*) in the Camargue:**

2 **duck guts are more important than their feet**

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## 26 **Summary**

- 27 1. Migratory waterbirds are major vectors for the dispersal of aquatic plants. However,  
28 quantitative field studies of the frequency of transport are scarce and the relative importance  
29 of internal and external transport remains unclear.
- 30 2. We quantified and compared the rates of internal and external transport of aquatic plant  
31 propagules by teal (*Anas crecca*) in the Camargue (southern France), inspecting the lower gut  
32 contents of birds that had been shot (n = 366) and washing birds that had been live-trapped (n  
33 = 68) during the winters of 2006-7 and 2007-8.
- 34 3. Intact propagules (n = 902) of 21 plant taxa were recorded in the rectum of teal, of which  
35 16 germinated or were shown to be viable. Intact propagules were recorded in the rectum of  
36 20% of teal, with up to 171 propagules per individual bird. *Chara oogonia* were most  
37 abundant (60% of intact propagules), suggesting that small size favours internal transport.  
38 *Eleocharis palustris*, *Juncus* spp. and *Potamogeton pusillus* (17%, 7% and 6% of intact  
39 propagules, respectively) were also very abundant.
- 40 4. Intact propagules (n = 12) of 10 plant taxa were found on the outside of live teal, and four  
41 of these taxa later germinated. Intact propagules were found on 18% of teal. No teal was  
42 found to carry more than one propagule externally. There was no difference in size between  
43 propagules transported internally and externally.
- 44 5. Teal are major dispersers of plants within the Camargue, despite being highly granivorous.  
45 Contrary to widespread assumptions in the literature, endozoochory by ducks appears to be a  
46 much more important mode of dispersal for aquatic plants than exozoochory. We found no  
47 evidence of changes in the probability of plant propagule dispersal at a landscape scale over  
48 the course of the winter, so propagule production and zoochory appear to be decoupled over  
49 time in aquatic systems.

50 **Introduction**

51 Passive dispersal of aquatic plants by birds is assumed to be a major ecological process,  
52 with advantages over dispersal via wind or water. Wind-dispersal is considered unfavourable  
53 for aquatic plants because it does not necessarily direct diaspores (the plant reproductive body  
54 and dispersal unit, i.e. seeds and oospores) towards aquatic habitats, whilst water-dispersal  
55 does not allow dispersal between waterbodies lacking a physical connection (Barrat-  
56 Segretain, 1996). Since aquatic plants often have a very large geographic range, ducks and  
57 other migratory waterbirds have long been proposed as major vectors for their dispersal  
58 (Darwin, 1859; Ridley, 1930). As these birds repeatedly move between different waterbodies  
59 at both local and broader scales, there is a relatively high probability that any propagules they  
60 carry will be dispersed to suitable habitat patches (Green, Figuerola & Sánchez, 2002). The  
61 ability of aquatic plants to undergo long-distance dispersal via migratory birds is likely to  
62 explain why they generally have a much wider geographical distribution than animals of a  
63 similar size (Fenchel & Finlay, 2004).

64 Plant propagules can be carried either in waterbird guts (“endozoochory” or internal  
65 dispersal) or attached on the outside of their body (“exozoochory” or external dispersal), and  
66 the latter has been widely assumed to be the most important process, especially because of the  
67 presence of small seeds in mud stuck to birds’ feet (Darwin, 1859; Ridley, 1930). However,  
68 most studies of either mechanism have been anecdotal in nature, and detailed quantitative  
69 studies in the field remain scarce (Figuerola & Green, 2002a). There have been particularly  
70 few studies of external transport (but see Vivian-Smith & Stiles, 1994; Figuerola & Green,  
71 2002b). Several recent field studies have quantified numbers of propagules in waterbird  
72 faeces and confirmed their viability (Figuerola, Green & Santamaría, 2002, 2003;  
73 Charalambidou & Santamaría, 2005; Sánchez, Green & Castellanos, 2006; Green *et al.*,  
74 2008). We are unaware of any previous studies comparing the importance of external and

75 internal transport simultaneously in a given bird population, though previous studies  
76 collectively confirm that dispersal mediated via waterbirds can be frequent in the field both by  
77 internal and external transport.

78 In this study, we investigated the role of teal (*Anas crecca* L.) as a dispersal vector of  
79 aquatic plant diaspores in the Mediterranean wetlands of the Camargue (southern France),  
80 comparing exo- and endozoochory. The Camargue area covers 140,000 ha in the Rhone  
81 Delta, and hundreds of thousands of ducks spend the winter there or stop to feed during  
82 migration. Teal are extremely abundant, representing 20 to 30 % of the wintering duck  
83 population and the annual peak count of this species averages 36,000 birds (Tamisier &  
84 Dehorter, 1999). Wintering teal in natural conditions feed mainly on aquatic plant propagules  
85 (Tamisier, 1971) and make regular movements between different waterbodies, spending the  
86 day on roosting sites and moving to feeding grounds at night (Tamisier, 1978). Experiments  
87 in captivity confirm that seeds can survive passage through the teal gut and be retained long  
88 enough to permit dispersal over hundreds of km or more during migratory flights  
89 (Charalambidou, Santamaría & Langevoord, 2003; Pollux, Santamaría & Ouborg, 2005). All  
90 these characteristics make teal likely vectors of plant propagules.

91 The main objective of this study was to quantify the rates of internal and external  
92 transport of plant propagules by teal within the Camargue. We quantified the presence of  
93 propagules in the lower gut and carried on feathers or feet, and tested their viability. We  
94 compared the frequencies of endo- and exozoochory for propagules of different sizes. We  
95 tested the hypothesis that smaller propagules were more likely to be dispersed externally,  
96 since they would be more likely to remain attached (Cousens, Dytham & Law, 2008).  
97 Although previous research has also suggested that smaller seeds are more likely to be  
98 transported internally (Soons *et al.*, 2008), we hypothesized that small seed size was more  
99 important in external than internal transport. We considered the importance of spatial and

100 temporal variation in rates of plant propagule transport. We tested the hypothesis that  
101 propagule dispersal would be coupled to propagule production, and would therefore be more  
102 frequent during the early part of the wintering period (see Clausen *et al.*, 2002). Finally, we  
103 reevaluated the importance of external *versus* internal plant propagule transport by ducks in  
104 the light of our findings.

105

## 106 **Methods**

### 107 *Collection and analysis of samples*

108 To study internal transport, the terminal part of the digestive tract (rectum) was extracted  
109 from teal shot at seven different hunting estates (Fig. 1), between September and January of  
110 the wintering seasons 2006-7 (n = 183 teal, hereafter the 2007 winter) and 2007-8 (n = 183  
111 teal, hereafter the 2008 winter) (Table 1). We focussed on the rectum because any intact  
112 propagules present in this part of the digestive tract can be considered to have survived gut  
113 passage (Charalambidou & Santamaría, 2002). Almost all birds were shot when flying out of  
114 feeding sites towards roosting sites, so that viable propagules in their rectum would very  
115 likely have been dispersed from one wetland to another. Ducks were sexed and aged using  
116 plumage criteria (Carney, 1992), although 2.2% of birds had an undetermined age. The  
117 rectum was removed by dissection, and then stored in a plastic bag in the fridge until analysis  
118 over the next few days. For statistical analyses, we pooled the few birds shot at sites 4 to 7.  
119 The upper gut contents of these same birds were used in a diet study (Brochet *et al.*,  
120 unpublished). Birds with a full oesophagus were preferentially selected for dissection in the  
121 2008 winter, which may explain why more plant propagules were found in the rectum in the  
122 second year (see Discussion).

123 To study external transport, samples were collected from 68 live teal captured for ringing.  
124 Teal were caught using standard baited funnel traps concealed in the vegetation (Bub, 1991),

125 at the Research Centre of Tour du Valat (Fig. 1), between October and March of 2007 (n = 10  
126 teal) and 2008 (n = 58 teal) (Table 1). Again, ducks were sexed and aged using plumage  
127 criteria, and the age of 1.5% of the birds was undetermined. Two samples were taken from  
128 each bird. First, samples from the feet were obtained by rinsing both feet into a plastic  
129 container. Then, samples from feathers were collected by brushing the whole plumage over a  
130 tray with a nylon bristle brush, then rinsing this material into a second plastic container. Using  
131 these techniques, we may have retrieved most or all propagules from the feet, but perhaps  
132 only the more easily detachable propagules from the plumage. It is possible that propagules  
133 deeply embedded in the plumage were missed (Vivian-Smith & Stiles, 1994). Samples were  
134 stored in the fridge before analysis during the next few days. We excluded from our dataset  
135 those seeds found on the outside of teal that may have come from bait used in the trap (*Oryza*  
136 *sativa* L., *Polygonum persicaria* L. and *Scirpus maritimus* L., but see Table 2 for details). Our  
137 bait was waste rice collected after the commercial harvest, hence the presence of rice weeds.

138 In the laboratory, samples were rinsed with mineral water through a 63- $\mu$ m sieve, and the  
139 residue was examined under a binocular microscope. Intact plant seeds and algal oogonia  
140 were separated from the residue. They were counted and identified using Campredon *et al.*  
141 (1982), Cappers, Bekker & Jans (2006) and a reference collection from the Camargue. Taxa  
142 whose intact seeds could not be identified were listed as unknown. All intact oogonia  
143 belonged to the genus *Chara* (*C. vulgaris* L., *C. globularis* Thuill. and *C. aspera* Deth. ex  
144 Willd. are the most frequent species in the Camargue, J.B. Mouronval pers. comm).

145 Propagule size (maximum length) was measured to the nearest 0.02 mm on graph paper  
146 under a binocular microscope for all taxa recorded. Ten propagules per species were  
147 measured, these being taken from the oesophagus of some of the same birds collected for the  
148 rectum sample. Oesophagus propagules provided a better estimate of size because they had  
149 not been subjected to mechanical erosion in the gizzard. Median values were used in

150 statistical analyses. The size of *Papaver* sp. and *Tamarix* sp. were taken from Cappers,  
151 Bekker & Jans (2006), because these species were absent from the oesophagus of teal  
152 analysed.

153

#### 154 *Germination and viability tests*

155 Intact propagules collected in the 2008 winter were germinated in microtitre trays with up  
156 to 10 propagules per cell, which was filled with mineral water. The *Chara* oogonia from a  
157 given individual duck were germinated in one or two small containers (diameter 6 cm, height  
158 5 cm), because oogonia tended to develop fungi when placed in microtitre trays. Trays were  
159 positioned in the laboratory at room temperature ( $20.6 \pm 0.3^{\circ}\text{C}$  [ $\bar{x} \pm \text{s.e.}$ ], ranging from 12° to  
160 32°C over the whole germination test period) and natural light condition. Germination was  
161 checked every 7 days for 56 days. At the same time, water was replenished and germinated  
162 propagules were removed. The few propagules that became infected by bacteria and/or fungi  
163 were immediately removed and the water of the cell refreshed. We did not apply antibiotics  
164 because increased infection risk is one of the processes affecting natural seed viability  
165 following gut passage (Figuerola, Green & Santamaría, 2002). After 56 days, non-germinated  
166 propagules were placed in the fridge for two months. Their germinability was then retested  
167 with the above protocol. After another 56 days, non-germinated propagules were dried at  
168 room temperature during one month and their germinability was then retested with the same  
169 protocol. Cold and dry periods were applied in order to break the dormancy of non-  
170 germinated seeds (Baskin & Baskin, 1998). After a final period of 56 days, propagules were  
171 tested for viability using a standard tetrazolium method (De Vlaming & Proctor, 1968; Holt-  
172 Mueller & van der Valk, 2002). By cutting propagules, embryos were exposed, and then were  
173 incubated on filter paper saturated with 1% tetrazolium solution in a Petri dish, for 24h in the  
174 dark at room temperature. Red staining indicated reduction of 2,3,5-triphenyltetrazolium

175 chloride by respiratory activity in the cells (Nachlas, Margulies & Seligman, 1960). Hence,  
176 propagules showing a positive tetrazolium response (*i.e.* with respiring embryos) were  
177 assumed to be viable.

178

### 179 *Statistical analyses*

180 We used a logistic regression with a binomial error distribution to model the probability  
181 that a bird had at least one intact plant propagule in its rectum as a function of the year of  
182 collection (2007 or 2008 winters), the site of collection (factor of four levels: site 1, 2, 3 and  
183 others), the day within the year at which it was examined (Julian date), sex (female or male),  
184 and age (juvenile, adult or undetermined). We analysed presence or absence rather than the  
185 number of propagules present owing to the high proportion of zeros (80 % of teal had no  
186 propagule in the rectum). The interaction Sex \* Age was also included. Day was included as a  
187 second order polynomial (*i.e.* adding Day<sup>2</sup> to the model) in order to take into account potential  
188 non-linear patterns across the wintering season. To reduce colinearity in polynomial models  
189 (see Legendre & Legendre, 1998), the 15 November was considered as day 0 (to divide the  
190 hunting season into two equal parts), earlier dates being considered as negative values. We  
191 carried out models for all plant species pooled together, then for *Chara* spp. and *Potamogeton*  
192 *pusillus* L. (the two most frequent species) separately. For each of the three cases, we tested  
193 all possible models (64 possible subsets of the six predictor variables). Then we used the  
194 Akaike Information Criterion (AIC) to compare different models. The best one has the  
195 smallest AIC value. However, if the difference of AIC ( $\Delta$ AIC) between two models was less  
196 than two, they were considered as equivalent (McCullagh & Nelder, 1989). As several best  
197 models were found, a model-averaging approach was carried out with all the best models  
198 (Burnham & Anderson, 2002). Final estimates and standard-errors of the parameters  
199 associated with each variable were thus obtained by weighting them across models with their

200 respective weight of AIC ( $\omega$ AIC). Higher  $\omega$ AIC resulted in a better explanation of the data  
201 variation by models. This last parameter was thus considered as evidence that the candidate  
202 model with higher  $\omega$ AIC was the best out of the set of models considered (Burnham &  
203 Anderson, 2002). Similar logistic regressions of the presence/absence of viable propagules  
204 were conducted for the 2008 winter for all plant species pooled, for *Chara* spp. and for  
205 *Potamogeton pusillus*, but no predictor variables had significant effects (results not shown).  
206 We did not carry out a similar logistic regression with plant propagules recorded externally  
207 because of the small sample size.

208       Given the high number of zeros, we used non-parametric Mann-Whitney U tests to  
209 compare the total number of intact or viable propagules in the rectum of teal from different  
210 years and/or for early and later parts of the winter season (comparing teal collected before and  
211 after 15 November). Similarly, Kruskal-Wallis tests were used to compare the number of  
212 propagules between collection sites, using pairwise *post-hoc* tests with sequential Bonferroni  
213 correction (Rice, 1989). Differences between years and early and late winter in the numbers  
214 of propagules recorded externally on teal were also tested with Mann-Whitney U tests.

215       To analyse the propagule viability in rectal samples (for data from the 2008 winter), we  
216 used a logistic regression with a binomial error distribution to model the proportion of viable  
217 propagules (summing germinated and non-germinated viable propagules) of *Chara* spp. (n =  
218 31 teal) and *P. pusillus* (n = 12 teal), as a function of the Day (Julian date) and Day<sup>2</sup>. The total  
219 number of intact propagules of each species found in the rectum was included in the logistic  
220 regression model as a binomial denominator. We applied the same method as for the previous  
221 logistic regression analysis.

222       To test the effect of propagule size on the kind of transport, we carried out a Fisher exact  
223 test to compare the proportion of propagules < 1, 1-2, and > 2 mm in length in rectal and  
224 external samples. A  $\chi^2$  test was not applied because some categories had low expected values.

225 R software (version 2.8.0) was used for all statistical analyses (R Development Core  
226 Team, 2008).

227

## 228 **Results**

### 229 *External transport*

230 Intact diaspores were not found externally on any of the 10 teal studied in 2007. In 2008,  
231 intact propagules of 10 taxa were found on a total of 12 of 58 teal, and four of these taxa later  
232 germinated (Table 2). No teal was found to carry more than one plant propagule. There was  
233 no evidence of a linear seasonal trend in the probability of carrying propagules (Mann-  
234 Whitney U test comparing the number of propagules present on teal before and after 15  
235 November for 2008: n = 27 and 31 teal respectively, U = 493, P = 0.121). Although only teal  
236 in the second winter carried some propagules, the difference between winters was not  
237 statistically significant (Mann-Whitney U test, n = 10 and 58 teal respectively, U = 220, P =  
238 0.086).

239

### 240 *Internal transport*

241 Intact diaspores of a total of 21 plant taxa were recorded in the rectum of teal, of which 16  
242 were later germinated or shown to be viable. Overall, intact propagules were recorded in  
243 19.9% of teal studied. *Chara* spp. was the most abundant taxon, representing 60.2% of all  
244 intact propagules and being present in 9.8% of teal (Table 3). *Potamogeton pusillus* was the  
245 most frequent of the remaining taxa and was recorded in 4.4% of birds, although *Eleocharis*  
246 *palustris* and *Juncus* spp. were more abundant in terms of total number of seeds (Table 3). Of  
247 propagules recorded in the 2008 winter, 38 % of *Chara* oogonia and 75% of seeds of other  
248 taxa germinated or were shown to be viable (Table 3).

249 We found 7, 7 and 12 best models of logistic regression for all propagule species  
250 combined, *Chara* spp. and *P. pusillus* respectively (see Appendix). A significant positive year  
251 effect was found for each dependent variable (Table 4), because the probability of the  
252 presence of plant propagules was consistently higher during the 2008 winter (27.9% of teal  
253 with intact propagules, compared to 12.0% in 2007). A significant site effect was also found  
254 for all plant species pooled (Table 4), owing to differences between sites in the frequency  
255 with which teal carried propagules in the rectum (Fig. 2). Tukey *post-hoc* tests suggested only  
256 one pairwise difference between sites 1 and 2 (n = 98 and 110 respectively; P = 0.052), with  
257 greater propagule presence in the former, though this was only marginally significant (Fig. 2).

258 Mann-Whitney U tests showed that the number of intact propagules in rectal samples in  
259 2008 was significantly greater than in 2007, for all propagules combined (U = 13810, P <  
260 0.001) as well as for *Chara* spp. (U = 14529, P < 0.001) and *P. pusillus* (U = 16013, P =  
261 0.04). Similar tests found no evidence of a seasonal effect, with no difference for either winter  
262 between the number of intact or viable propagules recorded in teal shot before or after 15  
263 November (all U-values < 4336, all P-values > 0.171).

264 When comparing differences in total number of propagules between sites with Kruskal-  
265 Wallis tests, there was a statistically significant effect in 2007 (2007:  $H_{3,183} = 12.794$ , P =  
266 0.005; 2008:  $H_{3,183} = 4.828$ , P = 0.074). This site effect was mainly due to the different  
267 proportions of teal carrying at least one intact propagule in the rectum (Fig. 2). *Post-hoc* tests  
268 showed that the only significant pairwise difference was between sites 1 and 3, (n = 55, 40  
269 respectively, U = 1360, P = 0.006) with more propagules in the former ( $\bar{x} \pm$  s.e. of number of  
270 propagules per bird:  $0.62 \pm 0.03$  and  $0.00 \pm 0.00$ , respectively).

271 When analysing with logistic regression the proportion of intact propagules in rectal  
272 samples that were viable, we found no significant effect of the Day or Day<sup>2</sup> for *Chara* spp. or  
273 *P. pusillus* (all P-values > 0.1).

274

275 *Propagule size effect*

276 The size range of propagules transported internally and externally was very similar (Fig.  
277 3) with no significant difference in the proportion of propagules of different size classes  
278 between transport modes (Fisher exact test:  $P = 0.350$ ).

279

280 **Discussion**

281 To our knowledge, this study is the first to make such a detailed comparison of rates of  
282 internal and external transport of plants by waterbirds. Since birds were shot when flying  
283 from feeding sites towards day-roosts, viable propagules in their rectum were very likely to be  
284 dispersed from one wetland to another. Teal at the site for live-trapping are also known to  
285 move between different wetlands on a daily basis. Moreover, teal undergo long-distance  
286 movements. There are approximately 2 million teal wintering in Europe (Wetlands  
287 International, 2006), many of which undergo long-distance migrations to the Camargue and  
288 other areas. Long-distance dispersal of propagules between the Camargue and other areas is  
289 favoured by the important fraction of propagules retained in the gut for 12 h or more  
290 (Charalambidou, Santamaría & Langevoord, 2003; Pollux, Santamaría & Ouborg, 2005;  
291 Brochet *et al.*, unpublished). Long-distance dispersal can occur throughout the winter, as there  
292 is a high turnover rate within the teal wintering population (Pradel *et al.*, 1997) and teal often  
293 move away from the Camargue in response to weather (Ridgill & Fox, 1990).

294 Our study suggests that teal are dispersers of many different aquatic plants within and  
295 beyond the Camargue wetlands. We detected intact propagules in the rectum or on the outside  
296 of 20% and 18% of teal, respectively, although more propagules were found in the rectum and  
297 these figures underestimate the numbers transported internally (see below). Previous field  
298 studies have used different methods that are not readily comparable, but propagules have been

299 found in 12% to 50% of teal faecal samples, varying according to sites and seasons  
300 (Figuerola, Green & Santamaría, 2003; Charalambidou & Santamaría, 2005). We are not  
301 aware of previous quantitative studies of external transport in teal, but small numbers of seeds  
302 were recorded on most waterbirds studied by Vivian-Smith & Stiles (1994) and Figuerola &  
303 Green (2002b).

304 We identified 21 plant taxa in the teal rectum, including the exotic species *Ludwigia*  
305 *peploides*, *Paspalum distichum*, *Heteranthera reniformis* and *H. limosa*. These species are not  
306 native to Europe and were introduced in the Camargue as ricefield weeds (Marnotte *et al.*,  
307 2006). Our results thus suggest that teal are important vectors of exotic species (see also  
308 Brochet *et al.* 2009). Many other plants are likely to be dispersed by the Camargue teal  
309 population, and we have detected propagules of an additional 57 plant taxa when analysing  
310 the foregut contents of teal included in this study (Brochet *et al.*, unpublished; see also  
311 Brochet *et al.* 2009). Most or all of these additional taxa can potentially undergo  
312 endozoochory by teal, and their absence from our rectal samples is explained by their relative  
313 rarity and the low probability of them being in the rectum at the particular time of our  
314 sampling. Diaspores are much more abundant in the oesophagus ( $1310 \pm 827 [\bar{x} \pm \text{s.e.}]$  (n =  
315 183 teal) and  $4857 \pm 1192$  propagules (n = 183 teal) in 2007 and 2008, respectively) and,  
316 unlike propagule size or hardness, abundance of a given taxon in the oesophagus is a  
317 significant predictor of its presence in the hindgut (Brochet *et al.*, 2009). Furthermore, in  
318 captive experiments 41% of diaspores fed to teal were recovered intact in faeces (Brochet *et*  
319 *al.*, unpublished).

320

### 321 *Relative importance of endo- versus exozoochory*

322 Our results suggest that, in general, internal transport is much more important than  
323 external transport for aquatic plants dispersed by ducks. We found both abundance (means of

324 2.5 *versus* 0.2 propagules per sample) and diversity (means of 0.3 *versus* 0.2 taxa per sample)  
325 of propagules to be higher in internal samples than in external samples. In addition, rates of  
326 internal dispersal were severely underestimated, as teal held many propagules further along  
327 the digestive tract that were likely to have been egested if they had not been hunted (see  
328 above).

329 Some idea of the actual extent of transport can be given as follows. At the time of  
330 collection, the gizzard and oesophagus of a teal contained only part of the daily intake of  
331 diaspores, since most are egested within 8 h (Charalambidou, Santamaría & Langevoord,  
332 2003; Pollux, Santamaría & Ouborg, 2005; Brochet *et al.*, unpublished). The teal we studied  
333 contained a mean of  $49 \pm 4$  intact *P. pusillus* seeds in the oesophagus and gizzard combined,  
334 and during an experiment in captivity 46% of *P. pusillus* seeds survived gut passage (of which  
335 78% were viable, Brochet *et al.*, unpublished). These figures are probably extreme values,  
336 because teal used in the feeding experiment were not used to feeding on seeds. However this  
337 would suggest that each teal could egest 17 viable *P. pusillus* seeds on a daily basis,  
338 equivalent to over 300,000 a day for the whole Camargue teal population.

339 Rates of exozoochoric dispersal are also likely to be underestimated to some extent in our  
340 study. We cannot rule out the possibility that some propagules became detached between  
341 entering the trap and being examined (birds were transported in mesh cages from the trap  
342 within the marsh to the ringing site on the shore). However, teal spend more than one hour per  
343 day preening their feathers (Tamisier & Dehorter, 1999) and are likely to detect and remove  
344 seeds quickly from their plumage (Sorensen, 1986). Our data, together with a review of  
345 literature, strongly suggest that the relative importance of exozoochory has been  
346 overemphasised in the past. For example, Ridley (1930) proposed that *Chara*, *Juncus* and  
347 *Myriophyllum spicatum* L. reach new wetlands on birds' feet, whereas we found all these taxa  
348 to be transported internally. Similarly, Carlquist (1967) proposed that *Eleocharis* and

349 *Ranunculus* are only transported externally by birds, but we found them to be transported  
350 internally. In contrast, our findings agree with those of Proctor (1962), who found *Chara*  
351 oogonia to be abundant in the lower guts of six waterbird species in North America, and  
352 argued that internal transport of oogonia is more important than external transport.

353 We found no evidence that exozoochory is relatively more important for smaller  
354 propagules than endozoochory. We may possibly have found a different result with a larger  
355 duck species such as mallard (*A. platyrhynchos* L.), since teal are the smallest European duck  
356 and tend to ingest relatively small propagules (Pirot, Chessel & Tamisier, 1984; Guillemain &  
357 Fritz 2002). However, small size is considered to improve the dispersal potential of seeds in  
358 both aquatic (De Vlaming & Proctor, 1968; Holt-Mueller & van der Valk, 2002, Soons *et al.*,  
359 2008) and terrestrial systems (Traveset, 1998), not only due to their large numbers (that  
360 increases overall dispersal probability; Jakobsson & Eriksson, 2000), but also because small  
361 propagules are more likely to survive passage through the gizzard (Soons *et al.*, 2008). The  
362 dominance of *Chara* oogonia amongst the propagules we recovered supports the view that, as  
363 a rule in macroecology, smaller organisms are more readily dispersed (Fenchel & Finlay,  
364 2004). It is possible that, the smaller the propagule of an aquatic plant in the Camargue, the  
365 more likely that species is to be dispersed by teal both externally and internally.

366 Most of the propagules that were transported externally lacked hooks or other  
367 morphological adaptations for external dispersal (see Sorensen, 1986), and five of the eight  
368 identified taxa found externally were also found internally, suggesting that exozoochory is  
369 largely a secondary mechanism for taxa dispersed more often by endozoochory. *Papaver* sp.  
370 was one of three taxa only found externally, but we found and germinated one *Papaver* seed  
371 in a dropping collected from one of the live-trapped teal (results not shown), confirming the  
372 potential for internal transport of this species also. Of the other two, the ability of *Phragmites*  
373 *australis* seeds to survive gut passage has been shown experimentally (Soons *et al.*, 2008).

374 Overall, apart from size, seed morphology seems to be an unreliable predictor of which taxa  
375 are passively dispersed by birds or other means (see also Calviño-Cancela *et al.*, 2006;  
376 Brochet *et al.*, 2009).

377

#### 378 *Spatial and temporal variation in dispersal rates*

379 We found no change in the probability of passive dispersal by teal during the course of a  
380 given winter. This strongly suggests there is a decoupling in the timing of plant propagule  
381 production and their dispersal by birds in this system. This is largely because propagules can  
382 be ingested by ducks from the sediments or become attached to bird feet or feathers long after  
383 they have dropped from the mother plant (Green, Figuerola & Sánchez, 2002). Even for  
384 fleshy-fruited terrestrial plants dispersed by passerines, there is extensive decoupling between  
385 fruit production and rates of avian dispersal (Herrera, 1998). Thus, we found no evidence to  
386 support previous suggestions (Clausen *et al.*, 2002) that submerged macrophyte seed dispersal  
387 period is probably limited to the seed production period in later summer and autumn. Previous  
388 studies have also shown viable seeds to be abundant in duck faeces in late winter (Figuerola,  
389 Green & Santamaría, 2002, 2003).

390 There is annual and spatial variation in the availability of different plant foods and their  
391 presence in the diet of teal in the Camargue, so it is no surprise that we found differences  
392 between years and sites in the numbers of intact propagules present in the rectum. However,  
393 the difference between years is likely to be a consequence of our change in methodology.  
394 During the second year of collection, teal were partly selected on the basis of whether or not  
395 they had a full crop, as judged externally by palpation of the neck (so as to study their diet).  
396 Approximately 87% of teal were considered to have a full crop. Plant propagule abundance in  
397 the upper gut is a significant predictor of their presence in the lower gut (Holt-Mueller & van  
398 der Valk, 2002; Brochet *et al.*, 2009), and the number of propagules found in the teal

399 oesophagus was significantly higher during the second winter (see above). Hence, we were  
400 probably more likely to study teal holding propagules in their rectum during the second  
401 winter.

402

403 In conclusion, our data demonstrate that teal are major dispersers of plant diaspores,  
404 despite being highly granivorous. They can disperse propagules both internally and  
405 externally, but the former is quantitatively much more important, contrary to previous  
406 assumptions. Roughly 10 times as many diaspores were found in a teal rectum (mean of 2.5)  
407 as carried externally (mean of 0.2), and taking into account the propagules found in the higher  
408 gut that survive gut passage, as many as a thousand may be dispersed daily by each teal,  
409 equivalent to tens of millions at the scale of the teal population wintering in the Camargue.  
410 Propagule morphology may not affect the importance of internal versus external transport,  
411 and may not a predictor of which propagules are dispersed by teal, although teal  
412 predominantly disperse small seeds. There is significant spatial variability in transport rates  
413 between sites, but propagule dispersal occurs throughout the entire winter season and is  
414 decoupled from propagule production.

415

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426

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540

541 **Tables**

542 **Table 1.** Number of teal samples for internal and external transport collected each month in  
 543 both study winters.

Month	Rectum				Washing			
	2007 <sup>1</sup>		2008		2007		2008	
	(n = 183)		(n = 183)		(n = 10)		(n = 68)	
	Female	Male	Female	Male	Female	Male	Female	Male
September <sup>2</sup>	5	12	11	35	-	-	-	-
October	15	31	9	22	-	-	11	9
November	22	22	5	12	0	2	10	9
December	15	15	25	19	-	-	1	2
January	19	27	20	25	-	-	5	9
February <sup>3</sup>	-	-	-	-	2	3	2	0
March <sup>3</sup>	-	-	-	-	2	1	-	-

544 <sup>1</sup>September 2006 to March 2007.

545 <sup>2</sup> No washing samples were collected in September, because water levels were too low to use  
 546 the trap.

547 <sup>3</sup> No rectal samples were collected in February and March, because the hunting season closed  
 548 at the end of January.

549 **Table 2.** List of plant taxa of which propagules were found intact in teal washing samples (P: plumage and F: feet) for winter 2008 (n = 58 teal)  
 550 (WP: number of birds with intact propagules; TP: total number of intact propagules; N germ: number of propagules that germinated). None of the  
 551 propagules that failed to germinate were found to be viable with a tetrazolium test.

Plant family	Plant taxa	Location	Length (in mm)	WP	TP	N germ
Characeae	<i>Chara</i> sp.	F	0.58	1	1	0
Chenopodiaceae	<i>Salicornia</i> sp.	P	1.13	1	1	1
Cyperaceae	<i>Cyperus difformis</i> L.	F	0.64	1	1	1
	<i>Scirpus maritimus</i> <sup>1</sup>	P	2.48	1	1	0
Juncaceae	<i>Juncus</i> sp.	F	0.52	2	2	1
	<i>Juncus</i> sp.	P	0.52	1	1	0
Papaveraceae	<i>Papaver</i> sp.	P	0.95	1	1	0
Polygonaceae	<i>Polygonum persicaria</i> <sup>1</sup>	P	2.32	1	1	0
Gramineae	<i>Paspalum distichum</i> L.	P	2.72	1	1	0
	<i>Phragmites australis</i> (Cav.) Trin. ex Steud.	F	1.82	1	1	0
Tamaricaceae	<i>Tamarix</i> sp.	F	0.81	1	1	0
Unknown	Unidentified (2 taxa)	P	-	2	2	1
	Total			12	12	4

552 <sup>1</sup> These seeds were excluded from the totals and from further analyses as they may have come from bait used in the trap.

553 **Table 3.** List of plant taxa of which propagules were found intact in teal rectum samples for winters 2007 and 2008 (WP: number of birds with  
554 intact propagules; TP: total number of intact propagules; Max: maximum number of intact propagules in one bird; N germ: number of propagules  
555 collected in the 2008 winter that germinated; N viable: number of propagules collected in the 2008 winter that did not germinate but were shown  
556 to be viable by a tetrazolium test).

Plant family	Plant taxa	Length (in mm)	2007 (n = 183)			2008 (n = 183)			N germ	N viable
			WP	TP	Max	WP	TP	Max		
Characeae	<i>Chara</i> spp.	0.58	5	34	21	31	525	144	182	15
Chenopodiaceae	<i>Salicornia</i> spp.	1.13	-	-	-	1	1	1	1	0
	<i>Suaeda maritima</i> (L.) Dumort.	0.65	-	-	-	3	7	5	5	1
Cyperaceae	<i>Cyperus difformis</i> L.	0.64	3	6	4	2	20	19	19	0
	<i>Eleocharis palustris</i> (L.) Roem. & Schult.	1.33	3	23	21	5	130	34	112	11
	<i>Schoenoplectus mucronatus</i> (L.) Palla	1.90	-	-	-	1	2	2	2	0
	<i>Scirpus maritimus</i> L.	2.48	-	-	-	5	6	2	1	5
Gramineae	<i>Echinochloa crus-galli</i> (L.) P.Beauv.	3.92	4	7	3	2	2	1	1	0
	<i>Paspalum distichum</i> L.	2.72	1	4	4	2	2	1	0	0
Haloragaceae	<i>Myriophyllum spicatum</i> L.	1.84	1	1	1	2	6	4	3	1
Juncaceae	<i>Juncus</i> spp.	0.52	3	3	1	3	61	39	16	0
Leguminosae	<i>Trifolium repens</i> L.	1.28	-	-	-	1	1	1	1	0
Onagraceae	<i>Ludwigia peploides</i> (Kunth) P.H.Raven	1.23	-	-	-	1	1	1	0	0
Polygonaceae	<i>Polygonum lapathifolium</i> L.	2.10	2	2 <sup>1</sup>	1	-	-	-	-	-
	<i>Polygonum persicaria</i> L.	2.32	1	2	2	-	-	-	-	-
Pontederiaceae	<i>Heteranthera limosa</i> (Sw.) Willd.	0.75	1	2	2	-	-	-	-	-
	<i>Heteranthera reniformis</i> Ruiz & Pav.	0.64	-	-	-	3	4	2	4	0
Potamogetonaceae	<i>Potamogeton pusillus</i> L.	1.55	4	16	13	12	30	12	21	1
Ranunculaceae	<i>Ranunculus</i> spp.	1.12	1	1	1	1	1	1	0	1
Unknown	Unidentified (2 taxa)	-	1	1	1	1	1	1	1	0
	Total		22	102	22	51	800	171	369	35

557 <sup>1</sup>One of these *P. lapathifolium* seeds germinated after removal from the rectum.

558 **Table 4.** Results of model-averaging based on alternative models (see Appendix), presenting  
 559 final estimate ( $\beta$ ), standard-error (se) and p-value (s: significant, ns: non significant) for each  
 560 variable and for all plant species pooled together, then for *Chara* spp. and for *Potamogeton*  
 561 *pusillus*.

Variables	All plant species pooled			<i>Chara</i> spp.			<i>P. pusillus</i>		
	$\beta$	se	p	$\beta$	se	p	$\beta$	se	p
Year	1.334	0.478	s	2.570	0.824	s	1.354	0.460	s
Site	-0.311	0.152	s	-0.180	0.208	ns	-0.015	0.103	ns
Day	-0.0003	0.001	ns	-0.0002	0.001	ns	-0.004	0.004	ns
Day <sup>2</sup>	-0.00004	0.00006	ns	-0.0001	0.0001	ns	-0.00007	0.0001	ns
Age	-0.123	0.204	ns	-	-	-	0.813	1.333	ns
Sex	0.013	0.100	ns	0.046	0.194	ns	-0.029	1.318	ns
Age*Sex	-	-	-	-	-	-	-0.659	0.87	ns

562

563 **Figure legend**

564 **Figure 1.** Map of the Camargue showing the seven collection sites for rectum samples (dark  
565 circles) and the collection site for external transport (hatched square).

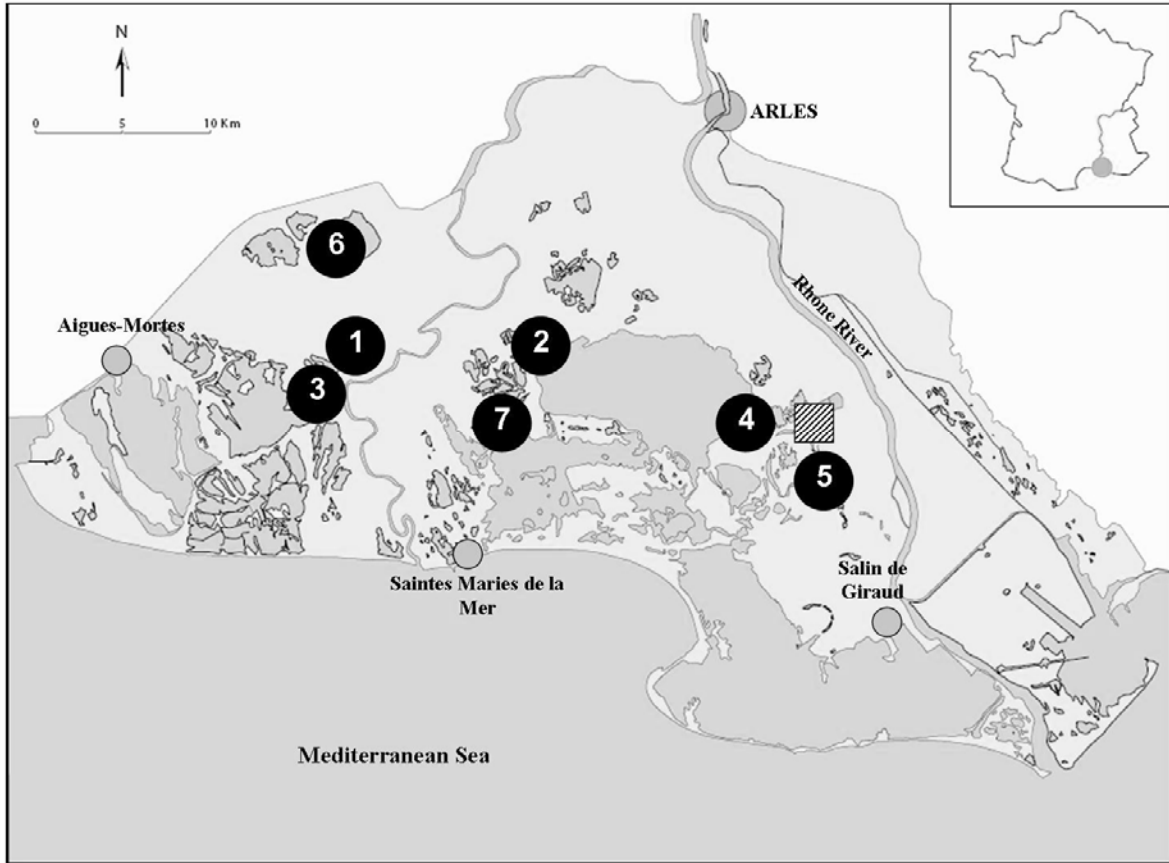
566

567 **Figure 2.** Proportion of teal with intact plant propagules in the rectum according to collection  
568 sites (Others: site 4 to 7, pooled together as relatively small numbers of teal were collected in  
569 these sites), for study winters 2007 (in grey) and 2008 (in white). Error bars indicate 95%  
570 Confidence Intervals. Sample sizes for 2007 and 2008, respectively, were: site 1, n = 55, 43;  
571 site 2, n = 41, 69; site 3, n = 40, 42; others, n = 47, 29.

572

573 **Figure 3.** Percentage of intact plant propagules found in teal rectums (grey) and external  
574 transport samples (white) according to size classes (< 1, 1 - 2, and > 2 mm in length).

575

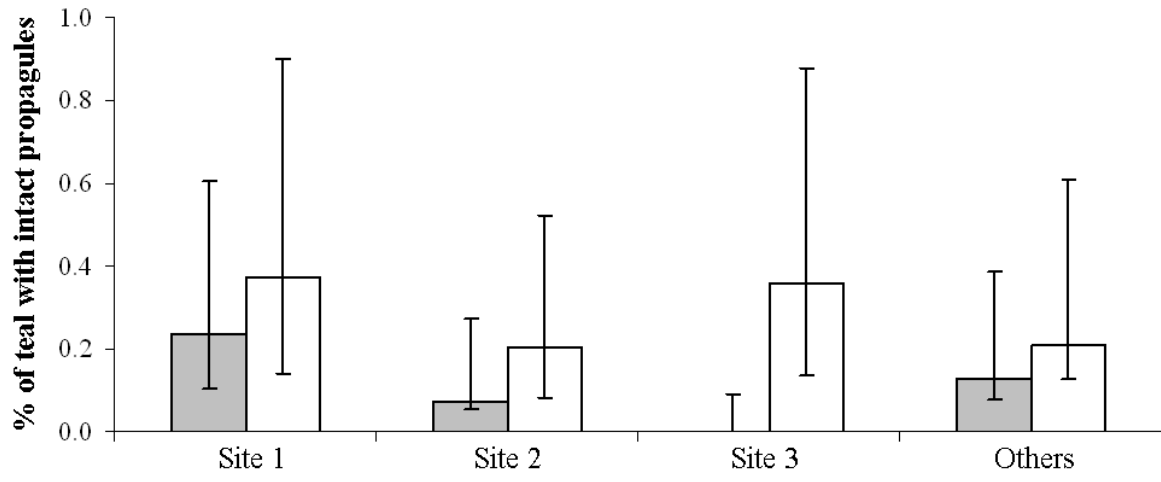


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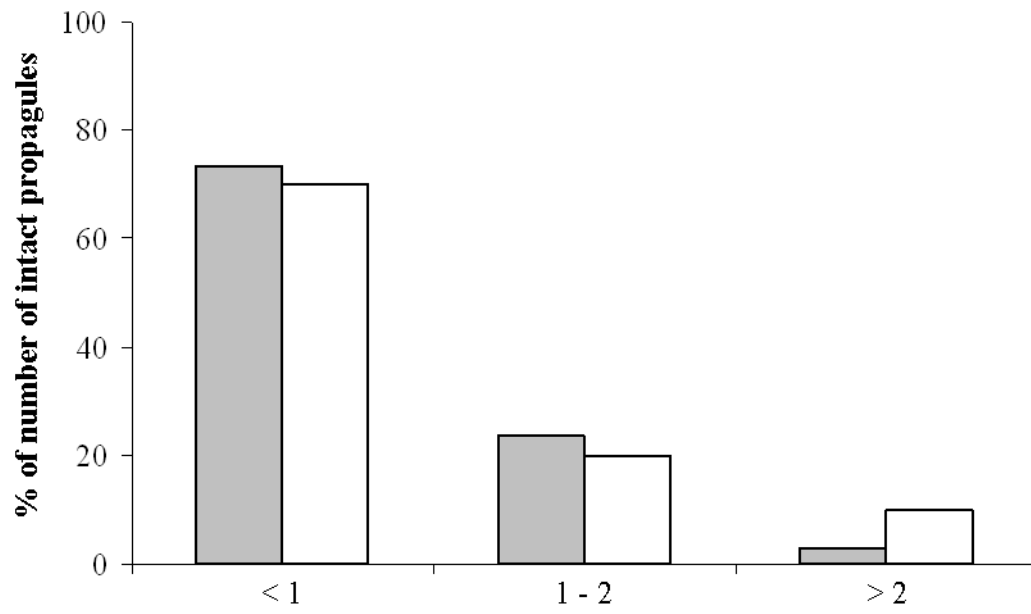
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585 **Appendix.** Null and best models ( $\Delta AIC < 2$ ) of logistic regression for the presence/absence of  
 586 plant diaspores in teal rectums, for all plant species combined, then for *Chara* spp. and for  
 587 *Potamogeton pusillus*, ranked in decreasing order of fit.

<b>Dependent variable</b>	<b>Models</b>	<b>AIC</b>	<b><math>\Delta AIC</math></b>
All plant species pooled	Year + Site	353.22	0.00
	Year + Site + Day <sup>2</sup>	353.84	0.62
	Year + Site + Age	353.90	0.68
	Year + Site + Day <sup>2</sup> + Age	354.25	1.03
	Year + Site + Day	354.64	1.42
	Year	355.02	1.80
	Year + Site + Sex	355.06	1.84
	Null model	367.74	14.52
<i>Chara</i> spp.	Year + Site + Day <sup>2</sup>	215.91	0.00
	Year + Day <sup>2</sup>	215.97	0.06
	Year	216.37	0.46
	Year + Site	216.44	0.53
	Year + Site + Day <sup>2</sup> + Sex	217.54	1.63
	Year + Site + Day + Day <sup>2</sup>	217.67	1.76
	Year + Day <sup>2</sup> + Sex	217.72	1.81
	Null model	237.31	21.40
<i>P. pusillus</i>	Year + Sex	129.95	0.00
	Year + Day + Sex	129.97	0.02
	Year + Day <sup>2</sup> + Sex	130.71	0.76
	Year + Age + Sex	130.8	0.85
	Year	131.08	1.13
	Year + Day + Age + Sex	131.09	1.14
	Year + Day <sup>2</sup> + Age + Sex	131.10	1.15
	Year + Day + Day <sup>2</sup> + Sex	131.14	1.19
	Year + Day <sup>2</sup>	131.34	1.39
	Year + Site + Day + Sex	131.55	1.60
	Year + Day + Day <sup>2</sup> + Age + Sex	131.87	1.92
	Year + Site + Sex	131.90	1.95
	Null model	133.45	3.50

588