

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- μ 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 Day² 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 (Δ 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 (ω AIC). Higher ω 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 ω 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 Day². 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 χ^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 ± 0.03 and 0.00 ± 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 Day² 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 ± 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 ± 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 ¹		2008		2007		2008	
	(n = 183)		(n = 183)		(n = 10)		(n = 68)	
	Female	Male	Female	Male	Female	Male	Female	Male
September ²	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 ³	-	-	-	-	2	3	2	0
March ³	-	-	-	-	2	1	-	-

544 ¹September 2006 to March 2007.

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

547 ³ 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> ¹	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> ¹	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 ¹ 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 ¹	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 ¹One 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 (β), 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>		
	β	se	p	β	se	p	β	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 ²	-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).

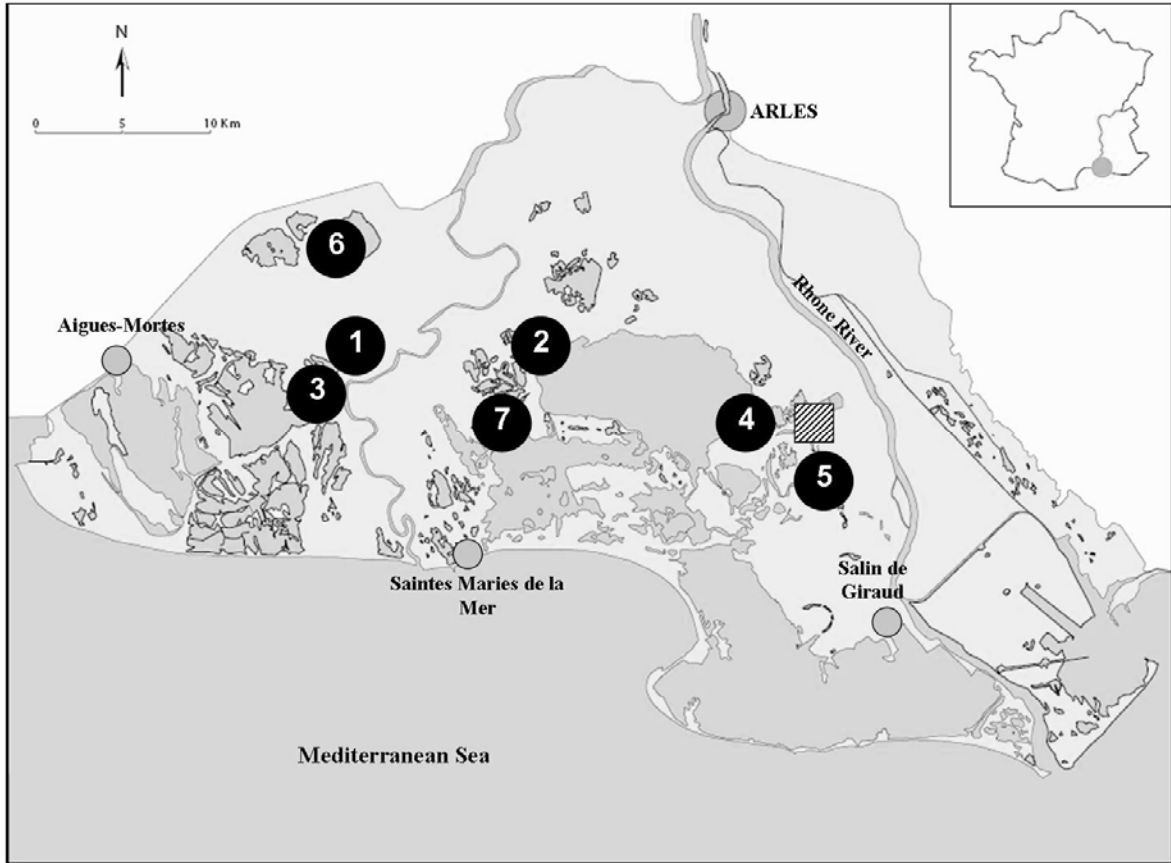
566

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).

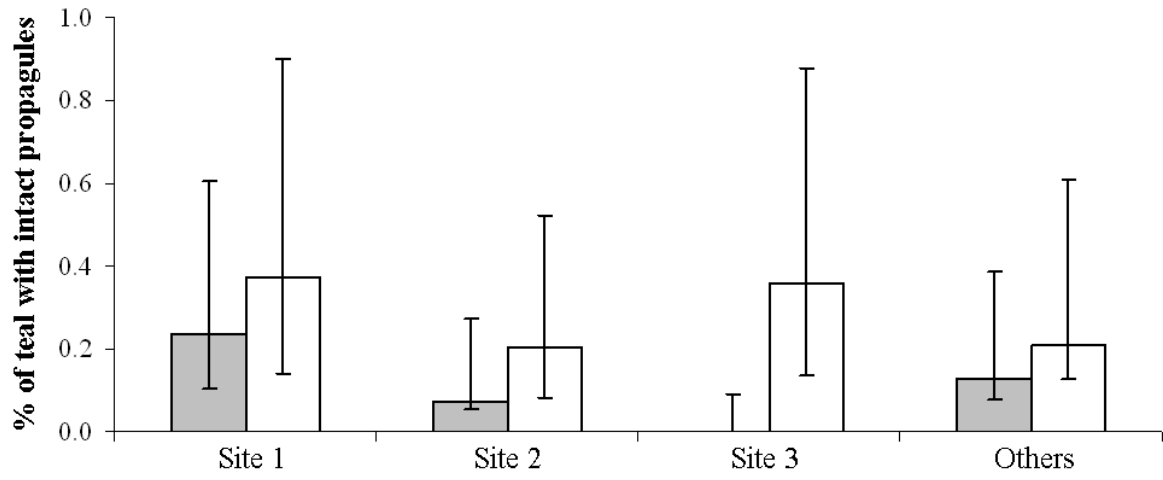
575



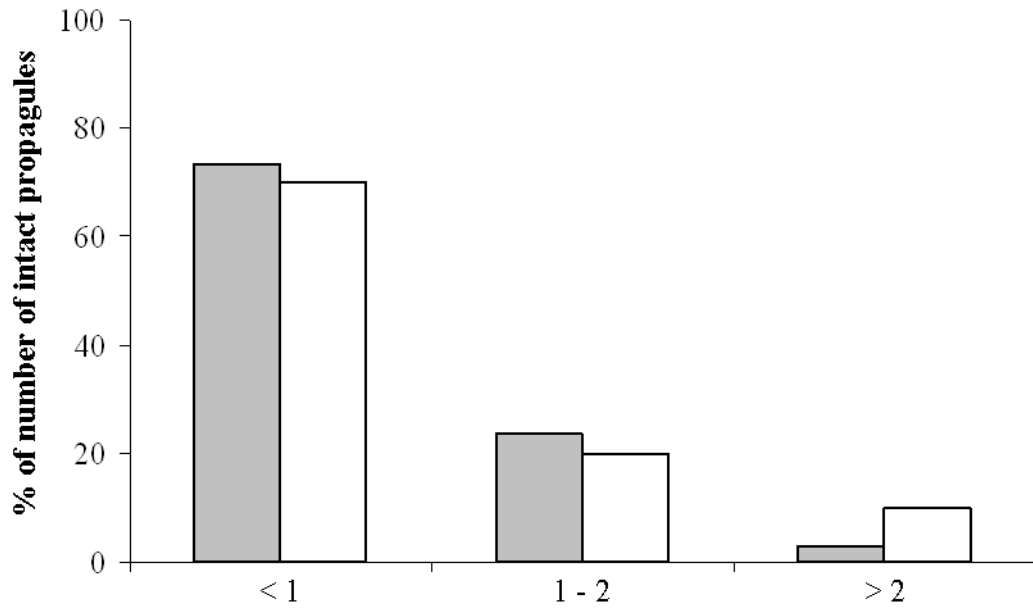
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585 **Appendix.** Null and best models ($\Delta AIC < 2$) of logistic regression for the presence/absence of
 586 plant diaspores in teal rectums, for all plant species combined, then for *Chara* spp. and for
 587 *Potamogeton pusillus*, ranked in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

Dependent variable	Models	AIC	ΔAIC
All plant species pooled	Year + Site	353.22	0.00
	Year + Site + Day ²	353.84	0.62
	Year + Site + Age	353.90	0.68
	Year + Site + Day ² + 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 ²	215.91	0.00
	Year + Day ²	215.97	0.06
	Year	216.37	0.46
	Year + Site	216.44	0.53
	Year + Site + Day ² + Sex	217.54	1.63
	Year + Site + Day + Day ²	217.67	1.76
	Year + Day ² + 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 ² + 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 ² + Age + Sex	131.10	1.15
	Year + Day + Day ² + Sex	131.14	1.19
	Year + Day ²	131.34	1.39
	Year + Site + Day + Sex	131.55	1.60
	Year + Day + Day ² + Age + Sex	131.87	1.92
	Year + Site + Sex	131.90	1.95
	Null model	133.45	3.50

588