



Passive internal transport of aquatic organisms by waterfowl in Doñana, south-west Spain

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ABSTRACT

Aim Waterbirds may play an important role in the maintenance of aquatic ecosystem biodiversity by transporting plants and invertebrate propagules between different wetlands. The aim of this study is to provide the first quantitative analysis of the transport of plant and animal propagules by a community of waterbirds.

Location Doñana marshes in south-west Spain.

Methods We quantified the number of intact seeds and invertebrate eggs in 386 faecal samples from 11 migratory waterfowl species (10 ducks and coot), collected from 3 November to 3 December 1998 (when birds were arriving from further north), and 22–25 February 1999 (when birds were leaving Doñana).

Results Intact seeds of at least 7 plant genera, and invertebrate eggs (ephippia of at least 2 crustacea, statoblasts of at

least 2 bryozoans and eggs of Corixidae) occurred in 65.6% of the faecal samples in early winter and 67.8% in late winter.

Main conclusions The abundance of different propagule types varied between waterfowl species in a seasonal and species specific manner, probably owing to differences in foraging strategies, bill and gut morphology, and seasonal shifts in propagule availability or distribution. Lamellar density was positively correlated with the abundance of intact propagules. Our results confirm that waterfowl play an important role in the dispersal of organisms in aquatic environments by internal transport. Wherever there is a propagule bank accessible to waterbirds, transport can occur even when propagule production and waterfowl movements do not overlap in time.

Key words Dispersal capacity, egg dispersal, endozoochory, gene flow, habitat colonization, passive dispersal, propagule transport, seed dispersal, Spain, waterfowl.

INTRODUCTION

Inland wetlands often constitute isolated habitats, yet many species of aquatic invertebrates and plants lacking active means of dispersal are found over huge geographical areas. Since Darwin (1859), the possibility that waterbirds transport seeds and invertebrates or their eggs has often been recognized (see also Salisbury, 1970; Galatowitsch & van der Valk, 1996; Bilton *et al.*, 2001). Experiments in captivity suggest that waterbirds can transport viable seeds or invertebrate eggs both internally or externally (see Figuerola & Green,

2002a for review). However, there is a need for much more quantitative information on the occurrence of waterfowl-mediated transport in the field (Figuerola & Green, 2002a; Green *et al.*, 2002).

In contrast to the abundance of studies on the dispersal of plants by animals in terrestrial habitats (see reviews in Janzen, 1983; Traveset, 1998), our understanding of the dispersal processes operating in wetlands remains extremely limited. Recently, Clausen *et al.* (2002) argued that the long distance dispersal of submerged macrophyte seeds by waterfowl was unlikely for several reasons, including the apparent temporal mismatch between propagule production and waterfowl movements. They also suggested that any transport would be unidirectional, occurring from north to south during autumn migration, but not from south to north during spring migration.

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Amongst dabbling ducks, considerable attention has focused on the influence of species variation in the density of the filtering lamellae within the bill on the size of invertebrates or seeds consumed. Green *et al.* (2002) recently speculated that species with a high lamellar density can be particularly important as vectors of small resting eggs that can resist digestion. High lamellar densities enable ducks to filter smaller particles (Crome, 1985), leading to negative correlations between lamellar densities and size of invertebrate prey and seeds in several field studies (Thomas, 1982; Nudds & Bowlby, 1984; Nudds, 1992; Nummi, 1993; Tamisier & Dehorter, 1999; but see Mateo *et al.*, 2000). However, ducks are highly plastic in their feeding behaviour and show great flexibility in their size selection in relation to food abundance. Denser lamellae appear to reduce the costs of filtering small items, but increase that of filtering larger items, and may often increase the variance in the size of items taken rather than decrease the average size (see, e.g. seed sizes recorded in different ducks by Thomas, 1982).

In this paper we examine the frequencies of plant and invertebrate propagules in the faeces of 10 species of ducks and *Fulica atra* (Table 1) in one of Europe's most important wetlands. We test the validity of two of the potential limitations to long distance dispersal by waterfowl proposed by Clausen *et al.* (2002):

- propagules are only transported at the time of their production;
- no propagules are transported during the northwards spring migration period.

To our knowledge, ours is the first field study to examine the interspecific and seasonal variations in the abundances of intact propagules in waterfowl faeces. We also investigate the relevance of bill morphology for explaining the interspecific differences observed.

METHODS

The study was conducted in Veta la Palma, a transformed marsh in Doñana (south-west Spain, Fig. 1), one of the most important areas for wintering waterbirds in Europe (Scott & Rose, 1996). Over a million waterbirds visit Doñana in a typical winter, many of them continuing further south into Africa. Veta la Palma is largely managed for extensive fish farming with *c.* 40 brackish, rectangular ponds with *c.* 100 ha surface each (total surface 3125 ha), and also includes 4442 ha of untransformed, temporary marshes. Islands are present in most ponds, and are used by roosting waterfowl during the day. During the study (winter 1998–99), most of the ducks wintering in Doñana concentrated in these ponds due to the scarcity of natural, seasonal habitats during a relatively dry winter. Waterbirds were counted monthly during the study as part of Doñana Biological Station's monitoring program (Table 1).



Fig. 1 Doñana holds a high diversity of fresh and brackish habitats used by many waterbirds during the winter and migration periods. The position of Veta la Palma is marked with a circle on the first picture. Source: Laboratorio de GIS y Teledetección and H Garrido/Seguimiento EBD.

Fresh droppings were collected from islands where waterfowl roosted. Samples were collected only from islands where the positions of birds could be accurately pinpointed (i.e. islands of bare mud interspersed with irregular patches of natural vegetation). With binoculars and a telescope we mapped the position of each individual using natural vegetation or small wooden stakes placed on each island as reference points. A first set of droppings was collected between 3 November and 3 December 1998, and a second set between 22 and 25 February 1999, referred to hereafter as early and late winter samples. These sampling periods overlapped with the autumn (southwards) and spring (northwards) waterfowl migrations.

Faecal samples (one dropping per sample) were stored in individual tubes in the refrigerator until analysis. Given the large number of birds at the study site (see Table 1), samples were likely to be from different individuals. Faeces were washed successively in a 0.5-mm sieve (large enough to retain

Table 1 Number of faecal samples examined for each waterfowl species in early and late winter in Veta la Palma (Doñana), mean number of intact propagules (\pm SD) and number of faeces with apparently viable propagules of each type (in brackets). The number of birds of each species counted in surveys of Veta la Palma coinciding with sample collection are shown in the last column. Data included in Fig. 2 have been omitted from the table, except for crustacea ephippia that are presented separately here for the distinct taxa

	Droppings examined	Droppings with propagules	Unidentified Leguminosa	<i>Scirpus</i> sp.	<i>Arthrocnemum</i> sp.	<i>Ranunculus scleratus</i>	Unidentified seeds	<i>Daphnia magna</i> ephippia	Ephippia of other Cladocera	Bryozoa statoblasts <i>Plumatella</i> spp.	Birds counted
Early winter											
<i>Anas acuta</i> Northern Pintail	16	10	0.4 \pm 1.8 (1)	0.8 \pm 3.3 (1)	—	—	0.3 \pm 0.7 (2)	0.1 \pm 0.3 (1)	0.1 \pm 0.3 (1)	—	41 345
<i>Anas clypeata</i> Northern Shoveler	24	16	0.5 \pm 1.3 (6)	—	0.1 \pm 0.2 (1)	—	0.5 \pm 1.1 (5)	0.1 \pm 0.5 (1)	1.7 \pm 4.3 (8)	—	90 141
<i>Anas crecca</i> Eurasian Teal	4	1	—	—	—	—	—	—	—	—	68 172
<i>Anas penelope</i> Wigeon	12	8	—	—	—	—	—	—	0.1 \pm 0.3 (1)	—	21 145
<i>Anas platyrhynchos</i> Mallard	36	14	—	0.1 \pm 0.2 (1)	0.1 \pm 0.4 (1)	0.1 \pm 0.3 (2)	—	0.1 \pm 0.2 (1)	0.1 \pm 0.2 (1)	0.1 \pm 0.2 (1)	58 365
<i>Anas strepera</i> Gadwall	17	12	—	—	0.1 \pm 0.3 (1)	—	0.2 \pm 0.4 (2)	—	—	—	3 465
<i>Aythya ferina</i> Pochard	15	10	—	—	—	—	—	—	0.1 \pm 0.3 (1)	—	10 470
<i>Fulica atra</i> Eurasian Coot	85	64	—	—	0.2 \pm 0.6 (5)	—	0.3 \pm 1.0 (13)	0.1 \pm 0.4 (6)	2.3 \pm 4.6 (28)	0.1 \pm 0.2 (2)	14 390
<i>Marmaronetta angustirostris</i> Marbled Teal	7	6	5.3 \pm 13.6 (2)	—	0.2 \pm 0.4 (1)	0.3 \pm 0.5 (2)	—	—	—	—	436
<i>Netta rufina</i> Red-crested Pochard	2	2	—	—	3.0 \pm 4.3 (1)	—	—	—	—	—	1 452
Late winter											
<i>Anas acuta</i>	28	25	0.1 \pm 0.4 (4)	—	—	—	0.3 \pm 0.7 (5)	—	0.3 \pm 0.6 (4)	—	2 498
<i>Anas clypeata</i>	14	14	—	0.1 \pm 0.3 (1)	0.3 \pm 0.6 (2)	—	6.8 \pm 12.6 (8)	0.9 \pm 1.6 (4)	19.3 \pm 34.1 (10)	—	8 902
<i>Anas crecca</i>	20	10	—	—	0.1 \pm 0.3 (1)	—	—	—	0.4 \pm 1.4 (3)	—	1 593
<i>Anas penelope</i>	4	3	—	—	—	—	0.8 \pm 1.5 (1)	0.3 \pm 0.5(1)	—	—	480
<i>Anas platyrhynchos</i>	51	40	0.1 \pm 0.4 (4)	3.1 \pm 0.2 (2)	0.4 \pm 1.5 (5)	—	0.4 \pm 1.1 (8)	—	0.2 \pm 0.6 (3)	—	14 443
<i>Fulica atra</i>	61	29	—	—	0.2 \pm 1.0 (3)	—	0.2 \pm 0.7 (6)	—	0.2 \pm 0.5 (7)	—	8 496
<i>Netta rufina</i>	2	0	—	—	—	—	—	—	—	—	25
<i>Tadorna tadorna</i> Shelduck	3	3	—	—	0.3 \pm 0.6 (1)	—	—	1.0 \pm 1.8 (1)	37.7 \pm 37.6 (3)	—	21

most seeds and large *Daphnia* ephippia) and a 0.04-mm sieve (to retain small propagules such as the oogonia of charophytes and resting eggs of zooplankton). The items remaining in the 0.5 mm sieve were examined immediately under a dissecting microscope. Items in the 0.04 mm sieve were fixed in 70% alcohol and examined later under the dissection microscope. Here we only present data for seeds and eggs that retained an intact cover and hardness and were considered to have survived the passage through the digestive tube. Taxonomic determination of retrieved seeds followed Cirujano (1986) for *Ruppia maritima*, following cultivation of germinated seeds; Castroviejo *et al.* (1986) for *Ranunculus*, also after cultivation; Campredon *et al.* (1982) for *Arthrocnemum* and *Salicornia* seeds and Characeae oogonia, and Alonso (1996) for crustacean ephippia.

We provide data on the presence of apparently viable propagules in the droppings rather than the results of germination assays, thus our data overestimate true viability. Since germination requirements are unknown for most of the species found in this study, this makes germination rate an underestimate of viability after ingestion (see Brock & Casanova, 1991 for a similar problem when estimating seed bank size). Furthermore, as examination of items retained in the 0.04-mm sieve was time consuming, fixation was required to prevent degradation of the samples. Data on the viability of *Ruppia maritima* seeds are presented elsewhere (Figuerola *et al.*, 2002).

Data on waterfowl lamellar density were obtained from Mateo *et al.* (2000). Since no information was available for *Marmaronetta angustirostris* we measured lamellar density from collection skins of 6 males and 6 females held in the collection of the Estación Biológica de Doñana. The distance between 20 consecutive lamella distal to the posterior end of the nostril was measured (see Mateo *et al.*, 2000) and expressed as lamella/cm.

Statistical analyses were restricted to bird species with at least five faecal samples examined in a given season. Data were analysed using general linear modelling in the SAS package (v8.2, SAS Institute, 2000), with a negative binomial error distribution and a log link due to the nature of the response variable analysed (count data with a dispersion much greater than expected for a Poisson distribution, see Bliss & Fisher, 1953). Spearman Rank correlation was used to test the relationship between mean abundance of propagules in faeces and the mean lamellar density of each duck species. This analysis was restricted to early winter because

only 4 duck species provided five or more samples in late winter.

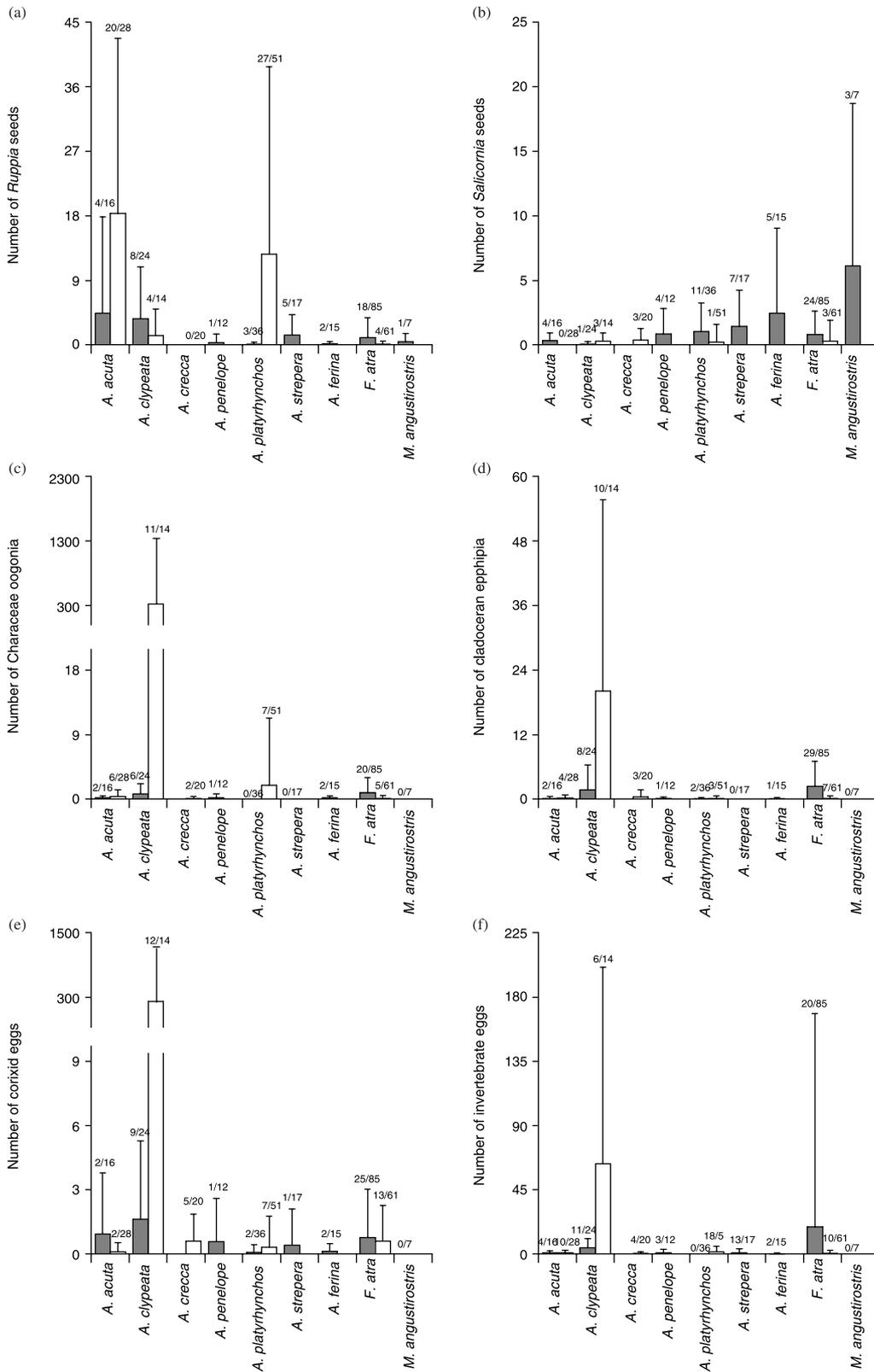
RESULTS

Intact propagules were found in 267 of the 401 faecal samples examined (66.6% overall, 65.6% of the 218 early winter and 67.8% of the 183 late winter samples). These included seeds of at least seven plant genera, Characeae oogonia, ephippia of *Daphnia magna* and other Cladocera, statoblasts of *Plumatella fungosa* and *Plumatella* spp. (Bryozoa), and eggs of corixids (*Sigara stagnalis* and *Sigara* sp.) and other invertebrates (Table 1 and Fig. 2).

Overall propagule abundance varied both between waterfowl species ($\chi^2 = 124.21$, d.f. = 8, $P < 0.0001$, Fig. 3) and seasons ($\chi^2 = 23.35$, d.f. = 1, $P < 0.0001$). A significant interaction was detected between these two factors ($\chi^2 = 100.84$, d.f. = 3, $P < 0.0001$). The number of propagules in *Anas acuta* droppings was similar in early and late winter ($\chi^2 = 2.57$, d.f. = 1, $P = 0.11$). Faeces of *Anas clypeata* and *Anas platyrhynchos* contained more propagules in late than in early winter ($\chi^2 = 37.67$, d.f. = 1, $P < 0.0001$), but the opposite occurred in *F. atra* ($\chi^2 = 61.75$, d.f. = 1, $P < 0.0001$). In early winter, propagule abundance was highest in the droppings of *F. atra* and *A. clypeata*, and lowest in the droppings of *A. platyrhynchos* (see Fig. 4). However, by late winter, propagule abundance was highest in *A. clypeata*, and lowest in *Anas crecca* and *F. atra*. Lamellar density was positively correlated with the abundance of intact propagules in the faeces ($r_s = 0.82$, $P = 0.02$, Fig. 5).

In the case of plants, apparently viable seeds of *Ruppia* sp. were the most prevalent propagule, found in 19.8% of samples in early winter and 31.6% in late winter. All or most of these seeds were *R. maritima*, the dominant submerged vegetation in the study site (identification was confirmed by the cultivation of 30 germinated seeds). Important differences in the abundance of *Ruppia* seeds between waterfowl species were detected ($\chi^2 = 71.76$, d.f. = 8, $P < 0.0001$). A trend for seasonal differences in the abundance of seeds ($\chi^2 = 3.89$, d.f. = 1, $P = 0.05$), and a species–season interaction were detected ($\chi^2 = 48.02$, d.f. = 3, $P < 0.0001$). These were the result of species specific patterns of seasonal variation, with an increase in the number of seeds in late winter *A. platyrhynchos* faeces ($\chi^2 = 40.06$, d.f. = 1, $P < 0.0001$), and a similar trend for *Anas acuta* ($\chi^2 = 3.21$, d.f. = 1, $P = 0.07$), but the opposite pattern for *F. atra* ($\chi^2 = 15.21$, d.f. = 1, $P < 0.0001$).

Fig. 2 Abundance of propagules of different species or categories (mean \pm sd) in the faeces of ducks sampled in early (■) and late winter (□). Only data for species with at least five samples collected in a given season are shown. Numbers over each bar indicate the number of samples in which propagules are present and the number of samples examined. (a) *Ruppia* seeds (b) *Salicornia* seeds (c) Characeae oogonia (d) ephippia of cladocera (e) eggs of corixids (f) unidentified invertebrate eggs.



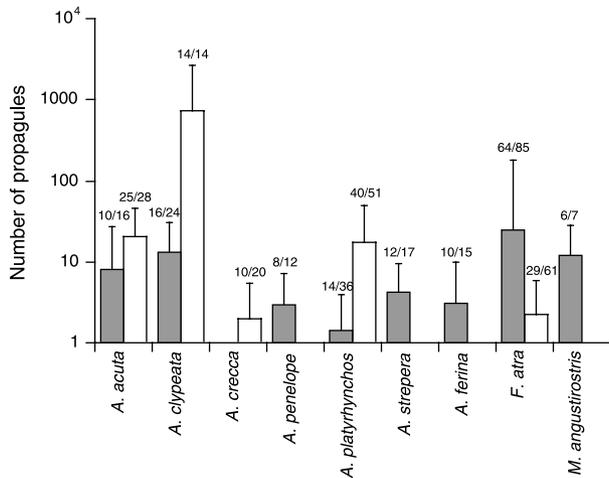


Fig. 3 Abundance of propagules (mean \pm sd) in the faeces of waterfowl sampled in early (■) and late (□) winter, plotted on a logarithmic scale. Only data for bird species with at least five samples collected in a given season are shown. Numbers over each bar indicate the number of faecal samples in which propagules were present and the number of samples examined.

Intact *R. maritima* seeds were most abundant in the droppings of *A. clypeata* during early and late winter samples, and no seasonal differences were apparent ($\chi^2 = 1.43$, d.f. = 1, $P = 0.23$, Figs 2a and 4). Intact *R. maritima* seeds were least abundant in the droppings of *A. platyrhynchos* in early winter, and were absent from the droppings of *A. crecca* in late winter.

The statistical models for *Salicornia* seeds had problems of convergence (i.e. to reach a stable solution by maximum-likelihood methods) probably due to the lack of seeds in the late winter samples. To solve this problem we removed *A. crecca* from the analysis, because it was the only species sampled in late winter without data for early winter. This analysis with a reduced number of waterfowl species identified interspecific differences in the abundance of *Salicornia* seeds ($\chi^2 = 20.07$, d.f. = 7, $P = 0.005$, Fig. 2b). Seeds were less abundant in late winter faeces ($\chi^2 = 4.05$, d.f. = 1, $P = 0.04$). There was a significant interaction between season and waterfowl species ($\chi^2 = 9.27$, d.f. = 3, $P = 0.03$). While *A. acuta*, *A. platyrhynchos* and *F. atra* showed fewer seeds in late winter ($\chi^2 > 4.08$, d.f. = 1, $P < 0.04$), no seasonal change in the abundance of seeds occurred in *A. clypeata* faeces ($\chi^2 = 1.84$, d.f. = 1, $P = 0.18$). In early winter, the abundance of *Salicornia* seeds was highest and lowest in the droppings of *M. angustirostris* and *A. clypeata*, respectively (Fig. 4). In late winter, the abundance of *Salicornia* seeds was highest and lowest in the droppings of *A. clypeata* and *A. acuta*, respectively.

The patterns for Characeae oogonia (Fig. 2c), ephippia (Fig. 2d), eggs of Corixidae (Fig. 2e), and unidentified

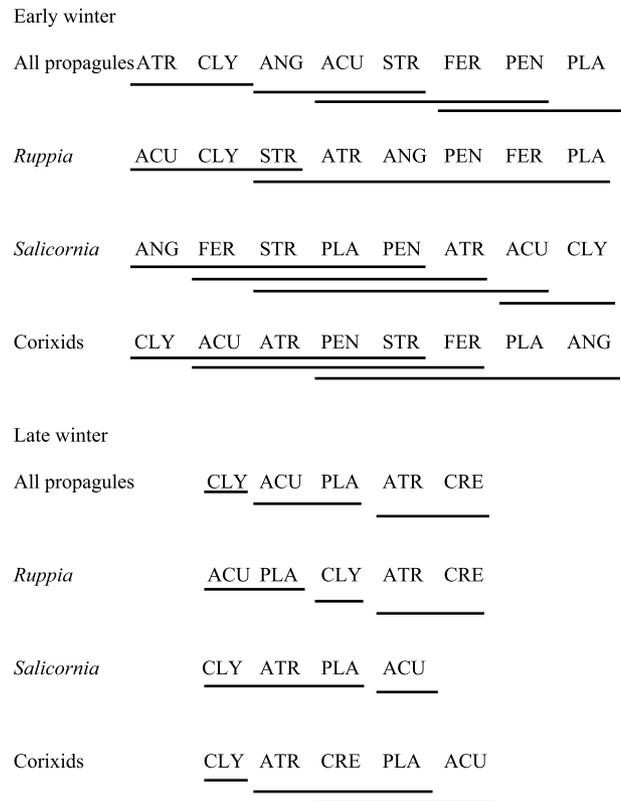


Fig. 4 Relative abundance of propagules in the faeces of each species and season. Species are ranked from higher (on the left) to lower abundance of propagules in their faeces and codes correspond to the first three letters of the specific Latin name. Differences between species and seasons were tested using the Wald χ^2 test (see Methods). Groups of species not presenting significant differences in the contrasts between them are joined by a horizontal line.

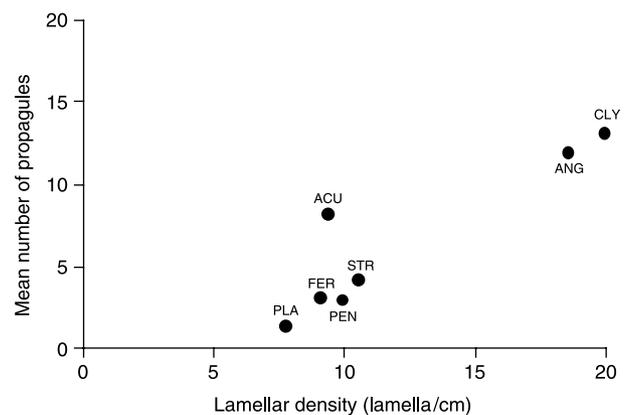


Fig. 5 Mean number of intact propagules recovered in the faeces of 7 duck species in early winter in Doñana in relation to bill structure considered as lamellar density (lamella/cm).

invertebrate eggs (Fig. 2f) were very similar to each other and for simplicity here we only present statistical analysis for eggs of Corixidae. Waterfowl species differed in the abundance of corixid eggs in the faeces ($\chi^2 = 96.06$, d.f. = 8, $P < 0.0001$), which also varied seasonally ($\chi^2 = 29.92$, d.f. = 1, $P < 0.0001$). A significant interaction between both factors occurred ($\chi^2 = 29.92$, d.f. = 3, $P < 0.0001$).

While no seasonal differences in abundance were detected in *A. platyrhynchos* and *F. atra* droppings ($\chi^2 = 2.79$, d.f. = 1, $P = 0.10$), corixid eggs were more abundant in the droppings of *A. acuta* in early winter ($\chi^2 = 4.64$, d.f. = 1, $P = 0.03$), and of *A. clypeata* in late winter ($\chi^2 = 36.41$, d.f. = 1, $P < 0.0001$). In early winter, the abundance of corixid eggs was highest and lowest in the faeces of *A. clypeata* and *M. angustirostris*, respectively (Fig. 4). In late winter, the abundance of corixid eggs was highest and lowest in the faeces of *A. clypeata* and *A. acuta*, respectively.

DISCUSSION

This represents the most extensive study to date of the internal transport of aquatic organisms by waterbirds and suggests that waterfowl can disperse large quantities of propagules. We found a high presence of undigested, apparently viable propagules in faeces during both early and late winter. Although by using apparent viability, instead of the results of viability assays, we have overestimated true viability, the number of propagules found in most of the cases was very high, suggesting that effective transport of viable propagules was taking place. The species potentially dispersed include submerged macrophytes (*R. maritima*), salt marsh plants (*Salicornia* sp. and *Arthrocnemum* sp.), bulrush (*Scirpus* sp.), amphibious plants (*Ranunculus scleratus*), and the eggs of corixids, cladocerans (*D. magna* and at least one other species) and bryozoans (*P. fungosa* and other species). Experimental evidence showing that propagules are viable after gut passage is available for most of these groups, with the notable exception of corixid eggs (see reviews in Charalambidou & Santamaría, 2002; Figuerola & Green, 2002a). The time the ingested seeds are retained in the digestive tract of ducks often exceeds 24 h (Swanson & Bartonek, 1970; Holt, 1999; Figuerola, 2002). Consequently, given the abundance and frequent daily movements of the migratory waterfowl in our study, the potential for dispersal is high, especially at a local scale (e.g. between the ponds in the study area and to other wetlands in Doñana). There is also a great potential for long distance dispersal given the long distance movements made by waterfowl passing through Doñana during autumn and spring migrations (Scott & Rose, 1996). Other waterbirds at Doñana, including waders and flamingoes, consume propagules, and would presumably be capable of transporting them long distances (Figuerola & Green, 2002a; Green *et al.*, 2002). The information available on the range of distances

potentially moved by waterfowl within the time period over which they retain propagules in the gut is scarce. However, analysis of *A. crecca* ringed in Denmark and recovered a few days later indicates that distances moved can sometimes exceed 100 km/day (Clausen *et al.*, 2002). One radio marked bird moved 1285 km in 24 h (from Denmark to western France, Clausen *et al.*, 2002).

Many authors have considered the potential for dispersal of seeds to be higher in autumn than in spring (e.g. Holt, 1999 and Clausen *et al.*, 2002 for aquatic habitats and Izhaki & Safriel, 1985 for terrestrial ecosystems), because plants and invertebrates tend to produce resistant propagules in autumn in seasonal, northern hemisphere environments. Although many of the propagules found in our study are only produced in late summer or autumn (e.g. *Ruppia* and *Salicornia*), our results refute this hypothesis. Some waterfowl species disperse more propagules in early winter, but others do so in late winter. The expected pattern of temporal variation in propagule transport was only supported for *Salicornia* seeds, which were most abundant in the droppings collected in early winter. *Salicornia* seeds are enclosed in the stems of the plant, and are ingested when birds feed primarily on these stems in autumn (van Eerden, 1984; Summers *et al.*, 1993; Green *et al.*, 2002). Most of the seeds we recovered in droppings were covered by fragments of digested stems. Enclosure of seeds within stems could favour the ingestion of the seeds, and enhance their passage through the digestive tract, particularly because *Salicornia* seeds lack the hard cover present in other types of seeds recovered from faeces (e.g. *R. maritima* and *Arthrocnemum* sp.). In late winter, no fresh *Salicornia* leaves are available for feeding, and the number of ingested seeds was reduced, although intact seeds were still found in late winter samples.

The observed seasonal changes in the prevalence of intact propagules in different waterfowl species are likely to be related to major changes in diets and foraging methods frequently observed between seasons (Batt *et al.*, 1992; Green *et al.*, 2002; Guillemain *et al.*, 2002). While pecking was the predominant feeding method in *Fulica atra*, duck species can also forage using the filter feeding strategy, and differences and seasonal changes in feeding depth can also occur. Since seasonal patterns of variation in the abundance of propagules in faeces differed between waterfowl species, this seasonal variability cannot be explained merely by changes in the abundance of propagules in the field. Other factors such as changes in habitat use, feeding methods, or the digestive handling of food could also influence seasonal patterns of propagule abundance in faeces. For example, species (or individuals) that feed on seeds or other hard foods develop stronger gizzards (more likely to destroy ingested propagules, see Figuerola *et al.*, 2002) than species or individuals that feed on softer prey (see review in Piersma *et al.*, 1993).

How seasonal changes in digestive efficiency can cause seasonal changes in the abundance of undamaged propagules in faeces is illustrated by a study of the diet of *M. angustirostris* in Morocco. Although more *Ruppia* and *Salicornia* seeds were consumed in October than in May, the number of intact seeds in faeces did not differ seasonally (Green *et al.*, 2002). In Doñana, we have also shown that the proportion of *Ruppia* seeds destroyed during digestion changes seasonally for some duck species (Figuerola *et al.*, 2002) and the same is probably true for other propagules found in the present study.

Local dispersal of propagules by waterfowl can influence the population structure of many plants and invertebrates but may also have important effects on propagule bank dynamics. Seed bank studies tend to ignore the role that movements by birds may play in these dynamics (e.g. Grillas *et al.*, 1993; González, 1999), and on temporal patterns of dispersal. Our results indicate that waterfowl consume and move an important number of propagules even five months after propagule production (see also Green *et al.*, 2002).

The widespread consumption of propagules in the sediments by waterbirds may result in major differences in the phenology of dispersal by aquatic and terrestrial birds. In the terrestrial communities studied until now, birds often ingest seeds to consume the surrounding fruit, or directly consume part of the seeds (Stiles, 2000; Willson & Traveset, 2000). However, waterbirds consume the recently produced propagules present in the water column and older propagules present in the upper sediment layer, either intentionally or unintentionally, e.g. while searching for invertebrates. While some of the seeds will be destroyed during digestion, others will pass through the digestive tube without damage.

Lamellar density appeared to explain some of the interspecific differences we found in the abundance of propagules in faeces in early winter. At least two not mutually exclusive factors may result in such a relationship. First, species with denser lamellae are more effective in retaining small particles (Crome, 1985; Nudds *et al.*, 2000). Second, lamellar density may be correlated with other characteristics of gut structure, since species with denser lamellae are likely to feed more on invertebrates and less on plants. In this case species with denser lamellae may destroy fewer propagules during digestion. We cannot separate the relative contribution of these two processes to our results. Furthermore, in the light of the great seasonal (and probably local) variability in the abundance of propagules, further research is necessary to establish how widespread is the relationship between lamellar structure and quantity of dispersed propagules.

The importance of dispersal limitation vs. local processes in the structuring of communities is an important topic in community ecology (Shurin, 2000; Shurin *et al.*, 2000). Our

results suggest that dispersal limitation is not a constraining factor for the distribution of the plant and invertebrate species found in our study, at least in areas with abundant waterfowl populations (supporting Shurin, 2000; Shurin *et al.*, 2000; but contrary to Dobson, 1992). Capacity to survive ingestion by waterbirds can be an important parameter to consider when discussing possible causes of interspecific differences in the ubiquity of aquatic organisms.

The overall effective movements of propagules in different directions will depend on a complex interaction between propagule characteristics, the abundance and behaviour of each dispersor species, and the survival and establishment probabilities of propagules transported in each season (De Meester *et al.*, 2002; Green *et al.*, 2002). The dynamics of the Doñana marshes and their waterfowl populations make it extremely difficult to quantify the probability for long-distance dispersal of a given propagule type in different directions. Annual and seasonal variations in the location and size of flooded areas, and the relative abundance and composition of propagule and waterfowl populations result in a wide array of potential interactions between propagules and dispersors at any given point in time.

In summary, waterfowl are likely to be major dispersors of plant and invertebrate propagules within, to and from the Doñana marshes by internal transport. This adds to evidence that waterfowl in Doñana transport propagules externally (Figuerola & Green, 2002b). The transport may occur throughout the winter, and is not only restricted to the time when propagules are produced. Thus, our results indicate that transport of propagules can occur both during autumn and spring migration. In addition to gut structure (see Figuerola *et al.*, 2002), bill structure may be an important factor explaining the potential of different waterfowl species to act as dispersors, with duck species with denser maxillary lamellae dispersing a larger number of propagules.

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