

The potential role of waterbirds in dispersing invertebrates and plants in arid Australia

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SUMMARY

1. The role of waterbirds as vectors of plants and invertebrates within and between arid-zone wetlands is poorly understood. We present the first detailed study of passive dispersal by nomadic birds in Australasia. We investigated the numbers and types of invertebrate and plant propagules within freshly collected faecal samples as well as their viability. We compared dispersal among Grey Teal (*Anas gracilis*), Eurasian Coot (*Fulica atra*) and Black Swan (*Cygnus atratus*) in the Macquarie Marshes, a complex of temporary to semi-permanent wetlands in New South Wales.

2. When faecal samples (n = 60) were inundated in the laboratory and monitored over three weeks, ciliates (75% of samples), nematodes (22%), ostracods (13%) and rotifers (5%) were recorded, with higher taxon richness in coot samples. Faecal samples (n = 71) were also sieved to quantify intact propagules, and ostracod eggs (70% of samples), large branchiopod eggs (31%) and bryozoan statoblasts (31%) were the most abundant invertebrates. Diaspores of 19 plant taxa were recorded, 14 of which were germinated in the laboratory or shown to be viable at the end of germination trials. The abundance and diversity of invertebrate propagules was highest in coot samples, whereas the abundance and diversity of diaspores was highest in teal samples.

3. One Australian Pelican (*Pelecanus conspicillatus*) sample was obtained and found to contain more taxa and far more propagules than any sample from other waterbirds, suggesting that piscivorous birds might have an important role in the indirect dispersal of propagules ingested by fish.

4. Our results support a role for birds in explaining the distributions of cosmopolitan plant genera such as *Lemna*, *Typha*, *Myriophyllum* and *Nitella*. The alien plants *Ranunculus sceleratus*, *Medicago polymorpha* and *Polygonum arenastrum* were recorded, demonstrating the potential role of waterfowl in the spread of exotic species. As the frequency and duration of flooding of arid-zone wetlands decreases owing to human activities, the importance of waterbirds in facilitating recolonisation of temporary wetlands is likely to increase.

Introduction

Temporary wetlands are the dominant wetland type in arid zones of Australia and other continents, but vary greatly in their frequency, duration and timing of flooding (Boulton & Brock, 1999; Porter *et al.*, 2001). Many aquatic plants and zooplankton survive intervening drought periods as dormant stages in long-lived propagule banks (Roshier *et al.*, 2001; Brock *et al.*, 2003; Boulton *et al.*, 2006; Jenkins & Boulton, 2007), or recolonise temporary arid-zone wetlands via hydrological connections, especially via floodwaters entering from rivers (Jenkins & Boulton, 2003). In addition, waterbirds can potentially transport plants and invertebrates between wetlands (Figuerola & Green, 2002a; Green *et al.*, 2002), although there is little information on the importance of such waterbird vectors in temporary wetlands.

In arid Australia, waterbird populations undergo boom and bust cycles and regular nomadic movements in response to the unpredictable changes in surface area and distribution of temporary wetlands suitable for feeding and breeding (Kingsford *et al.*, 1999; Kingsford & Norman, 2002; Roshier *et al.*, 2002). In more seasonal Holarctic environments, strictly migratory waterfowl (Anatidae and coot) are major dispersers of seeds and invertebrates between wetlands (Proctor, 1964; Holt-Mueller & Van der Valk, 2002; Figuerola *et al.*, 2003). In this study in inland south-east Australia, we investigated what plants and invertebrates are transported by nomadic waterbird species in their digestive systems. We aimed to identify and quantify propagules excreted by waterfowl, and to assess their viability through emergence and germination experiments. We compared the importance as vectors of ducks feeding in the sediments of flooded wetlands with that of grazing waterfowl. We also investigated whether fish-eating birds might indirectly disperse plant or invertebrate propagules, as proposed by Darwin (1859).

Methods

Collection of faecal samples

Samples of waterbird faeces were collected from the Macquarie Marshes in New South Wales on 27-28 July 2005. The Macquarie Marshes (30°35'S, 147°32'E) are a complex

of floodplain, lagoons and creeks (200,000 ha) with water regimes ranging from temporary to permanent (Paijmans, 1981). They are partly protected as a Ramsar site but are severely impacted by upstream dams and water extraction (Kingsford & Thomas 1995, Kingsford & Johnson 1998). Water levels were low at the time of our visit, and samples were collected from two semi-permanent lagoons where waterbirds concentrated; Buckuyinguy Swamp (31°02'S, 147°28'E) and Stock Lagoon (31°05'S, 147°30'E), separated from each other by 2 km.

Sixty Grey Teal (*Anas gracilis* Buller) faecal samples were collected from Buckuyinguy Swamp, 30 Eurasian Coot (*Fulica atra* Linnaeus) faecal samples were collected from Stock Lagoon, and 30 Black Swan (*Cygnus atratus* Latham) faecal samples were collected from both lagoons and flooded grassland located between them. One Australian Pelican (*Pelecanus conspicillatus* Temminck) sample was collected from Stock Lagoon. At the time of the sampling, approximately 150 teal, 150 coots, 200 swans and one pelican were in the study area. Teal were present at Stock Lagoon, but did not frequent accessible banks where faeces could be collected. The conductivity of water at Buckuyinguy Swamp was 362-440 $\mu\text{S cm}^{-1}$ (n = 4), and at Stock Lagoon was 522-737 $\mu\text{S cm}^{-1}$ (n = 4). Although Black Swans and coot have been classified as deep-water foragers (Roshier *et al.*, 2002), during our study they were grazing at the water's edge and out of the water in grassland. Teal were dabbling in the water column or in the sediments in the shallow parts of the lagoons.

Fresh faeces were collected from areas where monospecific flocks of birds were observed feeding or roosting out of the water. Each of the four species studied produced droppings with a distinctive size and colour. Fresh weight for each sample was 1.33 ± 0.11 g (mean \pm s.e., n = 16) for coot, 1.37 ± 0.07 g (n = 32) for teal, 10.5 ± 0.77 g (n = 23) for swans and 26.4 g for the pelican. The pelican sample was collected in the late afternoon from a log where the bird had roosted through the day. Samples from the other three species were collected from short, grazed grass and were usually not in contact with soil. Any part of the dropping in contact with soil was removed with a penknife and discarded to avoid contamination. It is unlikely that any individual bird was sampled more than once. Droppings collected were separated by at least 1 m. Each dropping was sealed in a plastic tube, then kept in a cool box with ice until we reached the laboratory at the University of New England.

Emergence of invertebrates from faeces

On 30 July 2006, about 0.3 g fresh weight from each of 30 grey teal, 15 Eurasian coot and 15 black swan samples was placed in a 70 cm³ vial together with 20 cm³ of mineral water (conductivity 467 $\mu\text{S cm}^{-1}$) to permit hatching of viable resting eggs. The lid was placed loosely on each vial to allow air exchange while reducing evaporation and the risk of aerial contamination by propagules. Ten controls were established with mineral water only, and ten (five from each lagoon) with mineral water and a similar quantity of the same type of shoreline vegetation (grasses) upon which most of the droppings had been deposited by the birds. Vials were randomly placed on the laboratory bench with a natural light schedule and temperatures oscillating from 15°C at night to 25°C during the day. The presence of live invertebrates was recorded for all vials using a binocular microscope (Leica MZ8, 10-50 x) on days 1, 3, 7, 14 and 21 after inundation. Total counts of invertebrates were made, except for abundance of protozoans that were estimated in the following abundance classes; 1-2, 3-10, 11-20, 21-50, 51-100, 101-200, 201-500, 501-1000, 1001-2000, 2001-5000, 5001-10000 and > 10000 per sample. However, since numbers may have been increased by reproduction after hatching, here we only present data on the presence or absence of each taxon in each sample.

Sieving for aquatic propagules

Remaining faecal samples were stored in the dark in a refrigerator at 2°C. Between 15 August and 20 September, we washed 30 teal, 20 coot and 20 swan samples and the one pelican sample through stacked 1 mm, 250 μm and 63 μm sieves using reverse osmosis water. Most of these faecal samples (27 of the teal, 14 of the coot and 14 of the swan samples) were the same ones used in the hatching experiment (i.e. we sieved that part of the sample remaining after removing part for the hatching experiment). Owing to their larger size, only 73.5 ± 5.1 % by fresh weight (mean \pm s.e., range 44-100%, n = 20) of swan samples and 51% of the pelican sample were sieved for propagules. Items retained on the sieves were placed in sample trays and inspected using a binocular microscope, removing apparently intact invertebrate propagules or plant diaspores that were then sorted and placed in tubes with a mixture of mineral water and reverse osmosis water. Eggs were returned to the refrigerator until they were measured, photographed and identified to the highest taxonomic resolution possible with the help of experts. Some were placed in filtered water from a nearby dam in Petri dishes at room temperature and any daily development observed. Photographs of eggs are available on request.

Germination from plant diaspores

We use the term diaspores from hereon as the plant dispersal units we recorded in faeces included fruits (e.g. Cyperaceae), mericarps (*Myriophyllum*) and oogonia (*Nitella*) as well as seeds (see results). Diaspores recovered from sieving were viewed under a binocular microscope for initial identification and assessment. Intact diaspores were placed in 30 ml of tap water in 6.5 cm diameter Petri dishes and incubated in germination cabinets set to 12 h of light at 25 °C and 12 h of darkness at 15 °C. Light was provided by fluorescent tubes emitting an intensity of $35 \mu\text{E m}^{-2} \text{s}^{-1}$ over the diurnal cycle. Emerging seedlings were potted into standard potting mix and grown in a glasshouse for identification. Where seedlings could not be successfully established, seeds were identified by comparing them with those on herbarium specimens at the NCW Beadle Herbarium UNE, or in the case of *Lemna disperma* Hegelm from published photographs of seeds (Cross, 2006). When germination trials were completed after about six months, all remaining diaspores were crushed to assess whether or not they were viable. Although most diaspores were rotten by then (see results), as well as data on the numbers of germinating and viable seeds, we present the total numbers of diaspores which appeared intact and potentially viable when initially extracted from faeces. We consider this justified because many diaspores rotten at the end of the study may have been viable at the moment of collection. Furthermore, these total numbers are more comparable with other studies of avian dispersal, which did not separate apparently whole seeds into viable and non-viable groups (e.g. Holt-Mueller & Van der Valk, 2002; Figuerola *et al.*, 2003; Charalambidou & Santamaria, 2005).

Statistics

We used 2x3 Fisher Exact tests (Lowry, 2006) to examine differences in the presence and absence of emerging invertebrates among teal, coot and swans. Chi-squared tests were not used owing to the high proportion of cells with expected values below five. We considered a taxon as present in a sample when it was recorded on at least one of the five days it was inspected. 2x2 Fisher Exact tests (StatSoft, 2001) were used to conduct pairwise post-hoc comparisons when significant differences between groups were recorded.

Owing to the abundance of zero values, we used non-parametric Kruskal-Wallis tests to compare the abundance and taxa richness of sieved propagules among teal, coot

and swans (StatSoft, 2001). Mann-Whitney U tests were used to conduct pairwise post-hoc comparisons when significant differences among groups were recorded.

Results

Emergence of invertebrates

Protozoans (ciliates), nematodes, ostracods and three rotifer taxa emerged from inundated waterfowl droppings (Table 1). No invertebrates emerged from any of the control samples, either those with water only or those with grass plus water. Protozoans were the group recorded in the highest proportion of samples, occurring in 83% of teal, 87% of coot and 47% of swan samples (Table 1, Fig. 1). These differences between bird species were significant (2x3 Fisher Exact test, $P = 0.029$). Post-hoc tests showed that the presence of protozoa was significantly lower in swan samples than in those from teal ($P = 0.016$) or coot ($P = 0.050$).

Nematodes were recorded in 60 % of coot, 20% of swan but only 3% of teal samples. These differences between species were highly significant ($P < 0.0001$). Post-hoc tests showed that the presence of nematodes was significantly lower in teal samples than in coot ($P < 0.0001$). Ostracods were recorded in 33 % of coot but only 7% of swan and teal samples, but these differences were not significant ($P = 0.055$). Two ostracod taxa were identified in our samples (S. Halse pers. comm.). The most abundant taxon (*Cyprinotus* sp.) was up to 1.7 mm in length with a pale orange colour. A much smaller number of *Cypretta* sp. were observed, with a hairy and pitted valve surface and dark green coloration.

Rotifers were absent from teal samples but recorded in 7% of swan samples and 13% of coot samples. These differences were not significant ($P = 0.12$).

Invertebrate propagules found by sieving

Numbers of invertebrate propagules (Kruskal-Wallis test, $H_{2,70} = 9.94$ $p < 0.007$) and numbers of invertebrate taxa ($H_{2,70} = 8.29$ $p = 0.016$) in faecal samples were significantly different among coot, teal and swans (Fig. 2). Coot samples contained significantly more propagules and more invertebrate taxa than swans or teal (Fig. 2), as confirmed by post-hoc tests ($P < 0.04$). However, the pelican sample contained as many taxa (5) and six times as many propagules as any other waterbird sample (Table 2). The

relative abundance of different taxa varied among bird species (Table 2). In particular, teal samples contained relatively more large branchiopod eggs and fewer bryozoan statoblasts than did swan and coot samples.

Ostracod cf eggs were soft and irregular in shape, 120-160 μm in diameter and pink-orange in colour. They were found both individually and in clusters of two to eight eggs, sometimes attached to fragments of vegetation. Their viability was confirmed when eggs left at room temperature developed two dark red, squarish eye spots within a week then a pair of legs or antennae within the egg within three more days. By that time, these latter structures had a dark pink outline but most of the egg was whitish and had lost its colour. These eggs were particularly abundant in coot samples (Table 2), supporting the view that they were ostracod eggs since ostracods (mainly *Cyprinotus* sp.) hatched with a higher frequency from coot samples (Table 1, Fig. 1).

Large branchiopod eggs were likely to be of *Branchinella* sp. (Anostraca, S. Halse pers. comm.) and were distinct brown or orange spheres or flattened spheres, typically 200-320 μm in diameter. Given their abundance in teal samples (Table 2), they were probably concentrated in sediments.

Bryozoan statoblasts were 360-440 μm in length and were floatoblasts belonging to an undescribed species of *Plumatella* (T.S. Wood pers. comm.). Their viability was confirmed when one of six statoblasts from the same coot sample placed at room temperature on 13/9/05 hatched after three days.

We could not satisfactorily divide cladoceran ephippia into different taxa, although it is likely that around four taxa were recorded. All but four ephippia had a single egg case, their length varying from 400-1200 μm . Double ephippia were 1000-1400 μm long and were likely to be of *Daphnia carinata* King (R. Shiel pers. comm.). We were unable to hatch any ephippia. Chydorids were often recorded intact but dead when faeces were sieved.

Plant diaspores

Intact diaspores of 19 plant taxa were recovered by sieving faecal samples, including 12 identified to species (Table 3). Germination was recorded in nine taxa, and another five taxa remained viable at the end of the germination trials (Table 4). Total numbers of diaspores (Kruskal-Wallis test, $H_{2,70} = 25.71$ $P < 0.0001$) and numbers of taxa ($H_{2,70} = 24.44$ $P < 0.0001$) in faecal samples were significantly different among coot, teal and swans (Fig. 3). This was because teal samples contained both significantly more

diaspores and more plant taxa than swans and coot (Fig. 3), as confirmed by post-hoc tests ($P < 0.0001$). However, the pelican sample contained more taxa and more than four times as many diaspores as any other waterbird sample (Table 3, Fig 3).

The relative abundance of different taxa varied among bird species (Table 3). The majority (62%) of diaspores found in teal samples were Cyperaceae, yet this family was not recorded in other birds. Many of the Cyperaceae diaspores had a black colour typical of those that have spent some time within sediments. *Ranunculus* seeds were recorded in 27% of teal samples, but were absent in other birds. *Typha* was the most abundant genus recorded in the single pelican sample and in swan samples, yet was absent in the teal samples. There was a striking similarity in the taxa recorded in coot and pelican samples, although abundance was much higher in the pelican sample. Larger diaspores with a length exceeding 1 mm were almost exclusively recorded in teal samples (Table 3).

Swan samples were dominated by shreds of grass leaves. Swan and especially coot samples contained large amounts of *Azolla filiculoides* Lamarck tissue, including clusters containing massulae and megasporocarps, some of which were potentially viable. Teal samples contained large amounts of live filamentous algae. Neither the algae nor the *Azolla* were quantified in our sieved samples. However, live filamentous algae were recorded in 43% of teal samples and 7% of swan samples during the emergence experiment.

Three alien species survived gut passage. Celery-leaved buttercup (*Ranunculus sceleratus* Linnaeus) seeds were in eight teal samples, one Burclover (*Medicago polymorpha* Linnaeus) seed was in a swan sample, and four oval-leaf knotweed (*Polygonum arenastrum* Boreau) seeds were in a swan sample (Table 3). Eight *R. sceleratus* seeds and one *P. arenastrum* seed germinated, whereas the *M. polymorpha* seed remained viable at the end of the germination trials (Table 4).

Discussion

Dispersal of propagules by waterbirds

As far as we are aware, this is the first field study of internal dispersal by waterfowl to simultaneously identify and test the viability of both invertebrate and plant taxa. The only previous field study of internal transport by Australian waterbirds was limited to

dispersal of *Eleocharis* by the relatively sedentary Purple Gallinule (*Porphyrio porphyrio* Linnaeus) in lakes of the Great Dividing Range in the New England tablelands (Bell, 2000).

Invertebrates emerged from 82% of our waterbird faecal samples in our hatching experiment, and we sieved invertebrate propagules or plant diaspores from 85% and 59% of our samples respectively. Each sample only held a small proportion of the daily faecal output for each bird. For example, since the daily faecal output for black swans is around 418 g fresh weight per day (Mitchell & Wass, 1995), each sample for the hatching experiment contained about 0.1% of daily output, and each sample sieved contained about 2%. Thus, our results show the great potential for colonisation of temporary wetlands by invertebrates and plants transported internally by birds. Dispersal of propagules externally on feet or in plumage is also likely to be important (Figuerola & Green, 2002a,b). When invertebrates, aquatic plants and waterfowl numbers increase greatly after flooding (Kingsford *et al.*, 1999; Boulton *et al.*, 2006; Brock *et al.*, 2006), there is potential for massive transport of invertebrates and plants.

The species in this study and most other Australian waterbirds are highly dispersive and nomadic (Marchant & Higgins, 1990; Kingsford & Norman, 2002; Roshier *et al.*, 2002). For example, grey teal can disperse up to 343 km in a day (Roshier *et al.*, 2006), enough to gradually spread plants or invertebrates between temporary wetlands over huge areas of arid Australia given the high levels of avian connectivity between wetlands at times of peak floods (Roshier *et al.*, 2001). All four waterfowl species studied have a continental distribution, while teal and pelicans occasionally move from Australia to neighbouring parts of Asia (Tracey *et al.*, 2004). Experimental data on retention times (Charalambidou & Santamaría, 2002; Holt-Mueller & Van der Valk, 2002; Charalambidou *et al.*, 2003b; Pollux *et al.*, 2005) suggest that invertebrates and plant diaspores can readily be transported in the gut of waterfowl for several hundred km. For example, the Bewick's Swan *Cygnus columbianus* Ord is a similar size to the Black Swan and has a retention time between 2.5 and 8 h when feeding on grass (B. Nolet pers. comm.) and a flight speed of 72 km/h (Welham, 1994).

Many of the birds we studied probably moved away from the Macquarie Marshes within days of our visit, or after heavy rains arrived the following month (Roshier *et al.*, 2002), spreading plants and invertebrates between wetlands. Waterbirds would also disperse these organisms within different parts of the extensive Macquarie Marshes, especially when inundated. However, if propagules of a given species are transported by

birds to new habitats, they may not become established there. Differences in the composition of aquatic communities are often better explained by local processes (competition, predation, differences in environmental conditions, etc) than by regional processes such as dispersal limitation (Langley *et al.*, 2001; Cottenie *et al.*, 2003). Our results suggest that such local processes explain the marked dissimilarity of community composition among closely neighbouring Australian wetlands (Brock *et al.*, 2003).

Since no invertebrates hatched in our controls, we are confident that our results are not seriously affected by contamination of propagules from bankside vegetation or from the air. Many propagules were clearly visible within the interior of the faecal samples. It is possible that higher rates of emergence from faecal samples in the hatching trials would have been recorded by maintaining them at lower temperatures than those used (Vandekerkhove *et al.*, 2005) or oxygenating the samples. The large branchiopod eggs did not hatch because they did not undergo the period of desiccation required to break diapause, although it is likely that many remained viable after gut passage (Sánchez *et al.*, 2007).

Migratory waterfowl in the northern hemisphere transport ciliates, ostracods, cladocerans, rotifers and nematodes internally (Green & Figuerola, 2005; Frisch *et al.*, 2007). Bryozoan statoblasts occur in faeces from a variety of European migratory waterfowl (Figuerola *et al.*, 2003; Figuerola *et al.*, 2004), and we confirmed their viability (see also Charalambidou *et al.*, 2003a). Waterbirds are widely assumed only to be important vectors for invertebrates with resistant, diapause eggs (e.g. Bilton *et al.*, 2001), yet we observed large numbers of apparently viable non-diapause ostracod eggs. Thus, egg morphology should not be considered a reliable indicator of avian dispersal potential (see also Bartholme *et al.*, 2005; Green & Sánchez, 2006).

Differing dispersal potential between waterbirds

Among the three main waterbird species, teal had a higher diversity and abundance of plant diaspores, whereas coot had a higher diversity and abundance of invertebrate propagules (as indicated both by sieving and hatching). Teal probably excreted more plant diaspores and large branchiopod eggs because they ingested them from the seed and egg bank when feeding in submerged sediments. In contrast, coot were mainly grazing on aquatic vegetation at the water's edge, and probably ingested many invertebrate propagules attached to this vegetation or floating at the water's edge. For example, the ostracod eggs were often attached to fragments of vegetation within the

faeces, and the *Plumatella* floatoblasts are likely to have been floating when ingested. Observed differences between waterfowl species may also be partially explained by differences in digestive efficiency. For example, invertebrate propagules may have had higher survival when passing through the digestive tract of herbivorous coot and swans, owing to lower efficiency digesting animal matter compared to omnivorous teal (Charalambidou *et al.*, 2005).

However, coot and teal samples were collected from different lagoons, and differences between sites in abundance of propagules may have contributed to differences among bird species. Invertebrate community composition in epibenthic cores taken at the time of our study (includes 1 cm mud and 250 ml water; see King 2004 for method) differed between the lagoons, with ostracods and *Brachionus* rotifers more common in Stock Lagoon, where the coot were feeding (authors, unpublished data). These taxa emerged more frequently from coot faeces. However, these lagoons were similar in total microinvertebrate densities (232 individuals/core at Buckuyinguy and 171 at Stock), water chemistry, habitat structure and composition, and both coot and teal samples were significantly different in propagule composition from the swan samples taken from both lagoons. Thus, differences between the lagoons cannot explain all the differences recorded between waterfowl species.

If bill morphology were all-important in determining which waterfowl species make good vectors, we would predict that teal would have both more plant *and* invertebrate propagules in their faeces. Their relatively dense lamellae in their bill for filtering food should favour ingestion of small particles, including propagules (Crome, 1985; Green & Figuerola, 2005). In contrast, we have found teal to be particularly important vectors of larger seeds, which are a major component of their diet (Marchant & Higgins, 1990). Evidently, in the absence of information on the spatial distribution of propagules, neither feeding method nor bill morphology reliably predict the importance of different, sympatric waterfowl species as dispersal vectors (see Green *et al.*, 2002 for further discussion). However, grazing waterfowl such as swans, coot and geese appear to be particularly good dispersers of *Plumatella* floatoblasts (Figuerola *et al.*, 2004).

Dispersal of alien and cosmopolitan plants

As far as we know, our study is the first to demonstrate that the cosmopolitan plant genera *Lemna*, *Typha*, *Myriophyllum* and *Nitella* are transported internally by

waterbirds. Given their ability to reproduce vegetatively from fragments, *Lemna*, *Typha* and *Myriophyllum* may also be dispersed externally on the feet or plumage of waterfowl (Sawada *et al.*, 2003). *Lemna* has been seen to be carried on the backs of waterfowl (Darwin 1859), but we are not aware of such direct evidence for *Typha* or *Myriophyllum*. Duckweeds have previously been assumed *not* to be seed-dispersed (Les *et al.* 2003), but we found *Lemna* seeds in faeces from three bird species. Molecular evidence strongly suggests that long-distance dispersal by birds over evolutionary timescales explains the cosmopolitan distribution of aquatic genera such as *Lemna* and *Myriophyllum* (Les *et al.*, 2003). Our findings suggest that diaspores transported internally may be more readily transported over long distances than vegetative parts carried externally and prone to desiccation. *Typha* seeds are generally assumed to be dispersed by wind (Cain *et al.*, 1998), but we found viable seeds in three bird species, suggesting that birds can be a main means of long-distance dispersal for seeds morphologically adapted for wind dispersal (Higgins *et al.*, 2003; Sánchez *et al.*, 2006).

Our results demonstrate the potential importance of waterbirds (*sensu* Wetlands International 2002) as vectors of alien plants (see also Powers *et al.*, 1978). All three of the exotic species we recorded are widespread and expanding in Australia (Western Australian Herbarium, 1998; DWBLC, 2005; Martin *et al.*, 2006) and are invasive in the USA (USDA-NRCS, 2007). *M. polymorpha* and *P. arenastrum* are not confined to wetlands, so waterbirds can disperse terrestrial alien plants as well as aquatic ones (see also Sánchez *et al.*, 2006). Wetland associated exotic plants can also be dispersed by terrestrial birds (Renne *et al.*, 2000).

Indirect dispersal by fish-eating birds

Darwin (1859) explicitly recognised that fish-eating birds may disperse propagules ingested by fish between different wetlands, yet this process has not previously been corroborated (but see Mellors, 1975). Our pelican sample contained over four times as many plant diaspores and six times as many invertebrate propagules as any other sample, even though we only sieved half of it. All the propagules were relatively small, and probably came from the gut contents of small fish. Such a large quantity of propagules was unlikely to be ingested incidentally (e.g. from sediments or water). *Lemna* and *Typha* seeds from pelican faeces were germinated, confirming that this nomadic fish-eater disperses plants. Such indirect or secondary dispersal also occurs in terrestrial systems (Nogales *et al.*, 2002). Future work should address indirect dispersal

by fish-eating birds, and assess its importance compared with that of waterfowl, shorebirds and other waterbirds (see Figuerola & Green, 2002a; Green *et al.*, 2002; Green & Figuerola, 2005 for reviews of dispersal by these latter groups).

Conclusion

This study extends our knowledge of the extraordinary role of waterbirds in connecting other organisms across wetlands that fluctuate in space and time. Birds are likely to be particularly important in facilitating the recolonization of invertebrates and plants with limited drought resistance in temporary wetlands after reflooding. The importance of this role is likely to be increasing over time as dam construction, extraction for agriculture and global warming cause the hydroperiods of Australian wetlands to decrease and the intervals between flooding events that physically connect different wetlands to increase (Kingsford & Johnson, 1998; Jenkins *et al.*, 2005).

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Table 1 Emergence of invertebrates in inundated samples of waterbird faeces, presenting numbers of samples for which each taxon was recorded on at least one of five observation days. No invertebrates were recorded in controls (see text).

Invertebrate taxa	Grey teal (n = 30)	Black swan (n = 15)	Eurasian coot (n = 15)	Total (n=60)
Protozoans (ciliates)	25	7	13	45
Nematodes	1	3	9	13
Ostracods	2	1	5	8
Rotifers- <i>Brachionus</i> sp.	0	0	2	2
Unidentified bdelloid	0	1	2	3
<i>Cephalodella</i> sp.	0	0	1	1
Total	25	9	15	49

Table 2 Invertebrate propagules and live adults recorded in waterbird faecal samples when sieved. Listed are the number of samples with propagules (*n* with eggs), the total number of propagules (Eggs) and the maximum number of propagules in any given sample (Max). Only propagules that were apparently intact are included.

Propagule type	Grey Teal (<i>n</i> = 30)			Black Swan (<i>n</i> = 20)			Eurasian Coot (<i>n</i> = 20)			Australian Pelican (<i>n</i> = 1)	Total (<i>n</i> = 71)	
	<i>n</i> with eggs	Eggs	Max	<i>n</i> with eggs	Eggs	Max	<i>n</i> with eggs	Eggs	Max	Eggs	<i>n</i> with eggs	Eggs
Large branchiopod eggs	15	56	10	2	2	1	4	4	1	12	22	74
Ostracod eggs cf	22	84	13	10	83	36	17	141	22	261	50	569
Bryozoan statoblasts	1	1	1	6	21	10	14	32	7	3	22	57
Cladoceran ephippia	4	7	3	3	3	1	4	6	3	12	12	28
Live nematoda ¹	-	-	-	-	-	-	2	4	3	0	2	4
Other unidentified eggs (5 types)	-	-	-	5	15	9	1	1	1	11	7	27
Total	26	148	23	14	124	50	19	188	23	299	60	759

¹Adults, not propagules.

Table 3 Intact seeds and other plant diaspores of different mean length (mm) recorded in waterbird faecal samples. Shown are the number of samples with apparently intact diaspores (WD), total number of diaspores (TD) and maximum number of diaspores in any given sample (Max).

Plant family	Plant species	Length	Grey Teal (n = 30)			Black Swan (n = 20)			Eurasian Coot (n = 20)			Australian Pelican (n = 1)	Total (n = 71)		
			WD	TD	Max	WD	TD	Max	WD	TD	Max	TD	WD	TD	Max
Cyperaceae	<i>Bolboschoenus fluviatilis</i>	3	19	81	19	-	-	-	-	-	-	-	19	81	19
	<i>Eleocharis acuta</i>	1.7	4	21	18	-	-	-	-	-	-	-	4	21	18
	<i>Eleocharis pallens</i>	1.2	1	2	2	-	-	-	-	-	-	-	1	2	2
	<i>Eleocharis sphacelata</i>	2.5	1	1	1	-	-	-	-	-	-	-	1	1	1
	<i>Schoenoplectus validus</i>	2.4	3	4	2	-	-	-	-	-	-	-	3	4	2
Gramineae	Unidentified Poaceae	<1	1	1	1	-	-	-	-	-	-	1	2	2	1
Juncaceae	<i>Juncus sp.</i>	<1	3	3	1	-	-	-	-	-	-	-	3	3	1
Lemnaceae	<i>Lemna disperma</i>	<1	3	3	1	-	-	-	1	1	1	3	5	7	3
Fabaceae	<i>Medicago polymorpha</i> ¹	1	-	-	-	1	1	1	-	-	-	-	1	1	1
Haloragaceae	<i>Myriophyllum crispatum</i>	0.5	9	40	16	1	1	1	7	14	7	38	18	93	38
Characeae	<i>Nitella sp.</i>	<0.4	2	4	2	1	2	2	-	-	-	2	4	8	2
Polygonaceae	<i>Polygonum arenastrum</i> ¹	2.2	-	-	-	1	4	4	-	-	-	-	1	4	4
Ranunculaceae	<i>Ranunculus sceleratus</i> ¹	<1	8	12	4	-	-	-	-	-	-	-	8	12	4
Portulacaceae	<i>Portulaca oleracea</i> cf	1	1	1	1	-	-	-	-	-	-	-	1	1	1
Typhaceae	<i>Typha dominguensis</i>	<0.5	-	-	-	-	-	-	1	1	1	3	2	4	3
	<i>Typha orientalis</i>	0.5	-	-	-	3	6	4	2	2	1	69	6	77	69
Unknown	Unidentified (three taxa)	1-3	2	2	1	2	2	1	-	-	-	-	4	4	1
Total			26	175	26	7	16	7	8	18	9	116	42	325	116

¹ Alien species native to Europe.

Table 4 Viability of plant diaspores recorded in waterbird faecal samples. Shown are the total number of apparently intact diaspores (TD), the number of diaspores that germinated (G) and the number that did not germinate but remained viable at the end of the study (V). All the other diaspores were found to be rotten by the end of the germination trials (see methods).

Plant family	Plant species	Grey Teal (n = 30)			Black Swan (n = 20)			Eurasian Coot (n = 20)			Australian Pelican (n = 1)			Total (n = 71)		
		TD	G	V	TD	G	V	TD	G	V	TD	G	V	TD	G	V
Cyperaceae	<i>Bolboschoenus fluviatilis</i>	81	10	5	-	-	-	-	-	-	-	-	-	81	10	5
	<i>Eleocharis acuta</i>	21	-	1	-	-	-	-	-	-	-	-	-	21	-	1
	<i>Eleocharis pallens</i>	2	1	-	-	-	-	-	-	-	-	-	-	2	1	-
	<i>Eleocharis sphacelata</i>	1	-	1	-	-	-	-	-	-	-	-	-	1	-	1
	<i>Schoenoplectus validus</i>	4	-	-	-	-	-	-	-	-	-	-	-	4	-	-
Gramineae	Unidentified Poaceae	1	-	-	-	-	-	-	-	-	1	-	-	2	-	-
Juncaceae	<i>Juncus sp.</i>	3	-	-	-	-	-	-	-	-	-	-	-	3	-	-
Lemnaceae	<i>Lemna disperma</i>	3	-	-	-	-	-	1	-	-	3	3	-	7	3	-
Fabaceae	<i>Medicago polymorpha</i> ¹	-	-	-	1	-	1	-	-	-	-	-	-	1	-	1
Haloragaceae	<i>Myriophyllum crispatum</i>	40	2	-	1	-	-	14	-	-	38	-	-	93	2	-
Characeae	<i>Nitella sp.</i>	4	-	1	2	-	-	-	-	-	2	-	2	8	-	3
Polygonaceae	<i>Polygonum arenastrum</i> ¹	-	-	-	4	1	-	-	-	-	-	-	-	4	1	-
Ranunculaceae	<i>Ranunculus sceleratus</i> ¹	12	8	-	-	-	-	-	-	-	-	-	-	12	8	-
Portulacaceae	<i>Portulaca oleracea</i> cf	1	-	1	-	-	-	-	-	-	-	-	-	1	-	1
Typhaceae	<i>Typha dominguensis</i>	-	-	-	-	-	-	1	1	-	3	-	-	4	1	-
	<i>Typha orientalis</i>	-	-	-	6	3	-	2	1	-	69	6	-	77	10	-
Unknown	Unidentified (three taxa)	2	1	-	2	-	-	-	-	-	-	-	-	4	1	-
Total		175	22	9	16	4	1	18	2	-	116	9	2	325	37	12

¹ Alien species native to Europe.

Fig. 1 Cumulative percentage of samples from which invertebrates emerged during days after inundating faeces of black swans, Eurasian coot and grey teal. See Table 1 for more details.

Fig. 2 (a) Number of intact invertebrate propagules sieved from each faecal sample for different waterbird species. Median number of propagules in any one sample was 1.5 for swans ($n = 20$), 9 for coot ($n = 20$) and 3 for teal ($n = 30$). (b) Number of invertebrate taxa (see Table 2) recorded per sieved faecal sample for different waterbird species. Medians were 1.5 taxa for swans, 2 for coot and 1 for teal.

Fig. 3 (a) Number of intact plant diaspores sieved from each faecal sample for different waterbird species. Median number of diaspores in any one sample was 0 for swans ($n = 20$) and coot ($n = 20$) and 3.5 for teal ($n = 30$). (b) Number of plant taxa recorded (see Table 3) per sieved faecal sample for different waterbird species. Medians were 0 for swans and coot and 2 for teal.





