

Implications of waterbird ecology for the dispersal of aquatic organisms

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Abstract

In this paper, we review some potential implications of waterbird ecology for their role as dispersers of aquatic plants and invertebrates. We focus particularly on internal transport (endozoochory) by the Anatidae (mainly ducks) and shorebirds, groups especially important for dispersal processes owing to their abundance, migratory habitats and diets. We conduct a literature review to assess the seasonal patterns shown by Anatidae in consumption of seeds and plankton, the interspecific patterns in such consumption (including the effects of body size, bill morphology, etc.), and differences in habitat use (e.g., shoreline vs. open water specialists) and migration patterns between species (e.g., true migrants vs. nomads). We show that many shorebirds are important consumers of seeds as well as plankton, and suggest that their role in plant dispersal has been underestimated. This review confirms that Anatidae, shorebirds and other waterbirds have great potential as dispersers of aquatic organisms, but illustrates how closely related, sympatric bird species can have very different roles in dispersal of specific aquatic organisms. Furthermore, great spatial and temporal variation is likely in dispersal patterns realized by a given bird population. We present evidence suggesting that northbound dispersal of aquatic propagules by endozoochory during spring migration is a frequent process in the northern hemisphere. Much more systematic fieldwork and reanalysis of the existing data sets (e.g., from diet studies) are needed before the relative roles of various waterbird species as dispersers can be fully assessed. © 2002 Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

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1. Introduction

There is substantial evidence from both field and laboratory studies that waterbirds disperse the propagules of many aquatic organisms, either externally (ectozoochory) by adhering to their feathers, feet or bill, or internally (endozoochory) via the digestive tract (see Figuerola and Green, 2002a; Charalambidou and Santamaría, 2002 for reviews). All waterbird (*sensu* Rose and Scott, 1997) groups (including shorebirds, rails, ibises, flamingos, etc.) are likely to be important for dispersal of propagules. Even the various groups of fish-eating birds are likely to be secondary dispersers of seeds, ephippia and other propagules found within their fish prey (Mellors, 1975).

In a recent paper (Figuerola and Green, 2002a), we reviewed direct evidence that waterbirds can disperse propagules both externally and internally. We do not repeat that evidence in this paper, though we do cite some

additional evidence that has recently come to our attention. Here, we will focus on the potential implications of some aspects of waterbird ecology for the dispersal of aquatic plants and invertebrates. We do not consider the important role of the functioning of the alimentary canal reviewed by Charalambidou and Santamaría (2002). We also try to minimize overlap with Clausen et al. (2002) who present a critical view of the potential for dispersal of submerged plants (Zosteraceae, Potamogetonaceae and Ruppiaceae) by Anatidae (especially geese and swans) in northern Europe, discussing various essential steps to effective long-distance dispersal. In contrast to Clausen et al. (2002), we do not limit our scope to this region, nor to this group of plants, nor to dispersal events exceeding 300 km (shorter dispersal events are also of great ecological importance). In addition, we include information on all kinds of aquatic plants and invertebrates in our review, and even include terrestrial plants. Many waterbird species are likely to play an important role in long-distance dispersal of terrestrial plants, as has been clearly demonstrated for yellow-legged gulls, *Larus cachinnans* (Nogales et al., 2001). Even in northern

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Europe, Anatidae are likely to have an important role in the dispersal of terrestrial seeds abundant in temporarily flooded grasslands (see, e.g., Thomas, 1982).

The Anatidae (ducks, geese and swans) are of particular importance for dispersal of other aquatic organisms because of their abundance, widespread distribution across the world's wetlands, as well as their tendency to show long-distance movements (del Hoyo et al., 1992). Furthermore, the importance of plant seeds and aquatic invertebrates in the diet of most Anatidae species makes them vectors for dispersal by internal as well as external transport (see Gaevskaya, 1966 for a review of the plant seeds consumed by various Anatidae and coot, *Fulica atra*). Owing largely to their importance as a hunting resource, a great deal of research has been conducted on Anatidae ecology, though this research has been focused largely on migratory species in the northern hemisphere (Baldassarre and Bolen, 1994). Almost nothing is known about the ecology of many of the large number of tropical and southern hemisphere species (Green, 1996), though we review the existing information below.

Very little has been published about the role of shorebirds in dispersal in the field. However, migratory shorebirds are likely to be particularly important for long-distance dispersal, because they are abundant (Rose and Scott, 1997) and often make non-stop flights of 4000 km or more (e.g., Piersma, 1987; Kvist et al., 2001). Unlike Anatidae, many shorebirds expel propagules in pellets as well as in faeces, potentially diversifying both retention time and propagule viability.

Most existing literature on waterbird ecology is based largely on an autecological perspective focusing on the nutritional or habitat requirements of the individual species and the implications for its management. The remaining literature tends to deal with the ecology of the waterbird community without considering its influence on other aquatic communities, e.g., via dispersal. The extensive literature on Anatidae diet usually provides no information as to whether or not seeds consumed survive digestion, or as to whether cladocerans or other invertebrates consumed contain resting eggs or not. Unfortunately, many papers even fail to distinguish between plant seeds and other parts of the plant, the objective being simply to identify those species that act as food plants for bird species of interest. However, our aim is to review the implications that much of this literature has for the role of waterbirds as dispersers of aquatic organisms via internal and external transport of propagules. We pay special attention to the dabbling ducks (tribe Anatini) and pochards (tribe Aythyini; see del Hoyo et al., 1992), which are the most abundant and most studied Anatidae on inland wetlands, as well as reviewing information on the nomadic, seed-eating whistling ducks (subfamily Dendrocygninae). We also review the literature on shorebirds.

2. Do shorebirds carry propagules?

A surprisingly large proportion of shorebird species, including many long-distance migrants, have been recorded consuming seeds (Table 1). After recording undigested seeds in guts, several authors (e.g., Alexander et al., 1996) have suggested that seeds are ingested to act as grit for breaking down animal food, though others (e.g., Davis and Smith, 1998) assume that they are consumed because of their high energy content, and some species are clearly seed or berry specialists. Saltmarsh seeds (mainly Chenopodiaceae) were found in 13–44% of droppings or pellets of five of eight shorebird species wintering in the Cádiz Bay, Spain (Pérez-Hurtado et al., 1997). In nearby Doñana, invertebrate eggs and saltmarsh seeds are carried externally by shorebirds (J. Figuerola and A.J. Green, unpublished). Phalaropes predate and can disperse ephippial *Daphnia* (Dodson and Egger, 1980).

Seeds of at least 122 genera of 48 families have been observed in the stomachs of common snipe (*Gallinago gallinago*) (Mueller, 1999). Some 31 species of seeds (mainly Poaceae and Chenopodiaceae) were found in 80 faecal samples of the plains-wanderer (*Pedionomus torquatus*) in Australia (Baker-Gabb, 1988). Seeds were abundant throughout the year, though *Atriplex* spp. was consumed mainly in autumn and winter.

Widgeongrass (*Ruppia maritima*) seeds were found in the faeces of knot (*Calidris canutus*) and curlew sandpiper

Table 1

Summary of the proportion of shorebird species from various families and subfamilies within major geographical regions that have been recorded as including seeds in their diet. We used a conservative approach, listing as 'not consuming seeds' also those species for which plant material is reported without explicitly specifying seeds

	Western Palaeartic ^a		Australasia ^b		North America ^c	
	Yes	No	Yes	No	Yes	No
PEDIONOMIDAE	–	–	1	0	–	–
ROSTRATULIDAE	1	0	1	0	–	–
JACANIDAE	–	–	1	0	1	0
BURHINIDAE	1	1	1	1	–	–
HAEMATOPODIDAE	0	1	0	5	0	2
RECURVIROSTRIDAE	2	0	3	1	2	0
DROMADIDAE	0	1	–	–	–	–
CHARADRIIDAE						
Charadriinae	5	5	8	5	7	2
Vanellinae	3	2	3	0	–	–
SCOLOPACIDAE						
Gallinagoninae	3	0	2	3	1	0
Scolopacinae	1	0	–	–	–	–
Tringinae	8	5	3	4	5	2
Arenariinae	1	0	0	1	0	1
Limnodrominae	–	–	0	1	1	0
Calidrinae	9	0	8	1	7	2
Phalaropodinae	2	0	–	–	2	0
GLAREOLIDAE	1	3	1	1	–	–

^a Data from Cramp and Simmons (1983).

^b Data from Marchant and Higgins (1993), Higgins and Davies (1996).

^c Data from Poole and Gill (1992–2000).

(*Calidris ferruginea*) (as well as whistling ducks) at coastal lagoons in Ghana during October–November (Ntiamo-Baidu et al., 1998). The seeds found in knot faeces were intact, but deposited in unsuitable habitat for *Ruppia* (T. Piersma, personal communication). The hooded plover (*Thinornis rubricollis*) also consumes *Ruppia* seeds (Marchant and Higgins, 1993).

Shorebirds have often been shown to consume seeds during migration. Baldassarre and Fischer (1984) found seeds to be important in the diet of five of nine wader species studied on autumn migration in September in the Texas Playa Lakes, comprising 19–37% of the aggregate percent gullet volume and occurring in 38–100% of individuals. Seeds included *Polygonum* spp. and *Scirpus* sp. Davis and Smith (1998) compared the oesophagus contents of American avocets (*Recurvirostra americana*), long-billed dowitchers (*Limnodromus scolopaceus*), least sandpipers (*Calidris minutilla*) and western sandpipers (*C. mauri*) on the Playa Lakes, and in total found more seeds on autumn (37–69% of birds) than on spring (8–30%) migration in all four species. However, *Amaranthus* and *Eleocharis* seeds were more abundant in spring in some species. Seeds (mainly *Potamogeton* and *Scirpus*) were found in 59–89% of gizzards of five species on autumn migration through Saskatchewan (Alexander et al., 1996).

Taris and Bressac-Vaquier (1987) found a major seasonal shift in seed consumption by black-tailed godwits (*Limosa limosa*) migrating through the Camargue. In spring 1986, none of 11 gizzards studied contained *P. pectinatus* seeds, yet they were the most abundant item in autumn, 1986 (268 seeds distributed between 10 of 14 gizzards studied). Small numbers of *Scirpus mucronatus*, *Alisma plantago-aquatica*, *Echinochloa crus-galli* and unidentified seeds were found in spring and small numbers of *S. maritimus*, *S. litoralis* and unidentified seeds were found in autumn. Black-tailed godwits wintering in Senegal fed almost exclusively on rice grain, with small amounts of natural seeds (Tréca 1984).

3. How do Anatidae morphology and microhabitat use influence transport of propagules?

The relative importance of plant material and invertebrates in the diet of Anatidae varies greatly according to species (Cramp and Simmons, 1983; Krapu and Reinecke, 1992; Marchant and Higgins, 1993; Baldassarre and Bolen, 1994; Higgins and Davies, 1996; Poole and Gill, 1992–2000). Some important sexual differences in diet occur (Krapu and Reinecke, 1992) which, owing to differences in movement behaviour between sexes (Baldassarre and Bolen, 1994), may translate into various sexual roles in dispersal. However, dietary differences between species are generally much larger than intraspecific sexual differences.

Body mass ranges over more than an order of magnitude in the Anatidae and, overall, there is a weak trend for larger species to feed on larger prey items (including seeds and

invertebrates). However, the radiation in bill morphology and associated foraging methods is more important as a predictor of ingestion rates of various items than body size itself. Bill size and morphology show only a weak relationship with body size (Kehoe and Thomas, 1987; Kooloos et al., 1989; Nudds et al., 1994; Green et al., 2001). Within the dabbling ducks, considerable attention has been paid to the importance of the variation in the density of the filtering lamellae within the bill and their influence on the size of invertebrates or seeds consumed by each species. Among northern hemisphere ducks, lamellar density is particularly high in the northern shoveller (*Anas clypeata*) and particularly low in the mallard (*A. platyrhynchos*) (Nudds et al., 1994). All four of the world's shoveller species plus the pink-eared duck (*Malacorhynchus membranaceus*) are well adapted to feeding on zooplankton (del Hoyo et al., 1992), and thus are likely to be particularly important as vectors of resting eggs that can resist digestion. The same is true of filter-feeding flamingos (Zweers et al., 1995).

High lamellar densities enable ducks to filter smaller particles (Crome, 1985), leading to negative correlations between lamellar densities and invertebrate prey size and seed size in several field studies (Thomas, 1982; Nudds and Bowlby, 1984; Nudds, 1992; Nummi, 1993; Tamisier and Dehorter, 1999). 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 various ducks by Thomas, 1982). Thus, in various studies, lamellar differences do not explain interspecific differences in size selection (see Mateo et al., 2000). Ducks have mechanisms of feeding on items smaller than the interlamellar gap (Kooloos et al., 1989; Gaston, 1992), though these mechanisms remain poorly understood. Correlations between lamellar densities and food size have only been established for north-temperate dabbling ducks and it remains unclear whether or not such relationships occur in other Anatidae (e.g., diving ducks) and in other parts of the world.

The densities of various plant and invertebrate propagules in wetlands tend to vary greatly from the shoreline to offshore, open microhabitats (with depth, nature of vegetation, etc.). The distribution of aquatic plant seed banks in relation to depth varies between plant species and wetland type (Pederson and van der Valk, 1984; Bonis et al., 1995), but in large wetlands with deeper, open centres both seeds and waterbirds tend to be concentrated around the shoreline facilitating the consumption and adherence of seeds.

Propagule distribution tends to be highly patchy (e.g., floating propagules become highly concentrated along the shoreline facing prevalent winds), but distribution patterns are highly specific to each propagule species and vary greatly over time. *Artemia* eggs concentrate into large

scums along the shoreline of salines where flamingos and shelduck (*Tadorna tadorna*) feed on them (MacDonald, 1980; Walmsley and Moser, 1981). There is evidence that dabbling duck species with fine lamellae spend more time in offshore, open habitats, whereas those with coarse lamellae spend more time in shoreline habitats (Nudds et al., 1994; Green, 1998a), a pattern likely to influence the propagules that may adhere to each species externally, as well as those that are ingested. The chances of external transport are obviously related to the use by waterbirds of habitats where adherent propagules or other transportees are abundant. Rogers and Korschgen (1966) comment on how *Gammarus* were frequently seen clinging to the belly feathers of preening lesser scaup (*Aythya affinis*) in lakes where these amphipods were abundant.

However, duck body size also has a strong influence on microhabitat use, larger dabbling species tending to feed at greater depths (Green, 1998b; Nudds et al., 2000). The depth distribution of propagules varies greatly between seasons (e.g. as propagules are produced near the water surface and later incorporated into the propagule bank in the sediments). It is thus no surprise that feeding behaviour of dabbling ducks also shows a marked seasonal shift, with feeding occurring at greater depths during the non-breeding/wintering period (Thomas, 1980, 1982; DuBowy, 1988). Eurasian teal (*Anas crecca*), mallard and pintail (*A. acuta*) wintering in western France switched to relatively deeper feeding methods (i.e., more neck dipping and upending sensu Green, 1998b) as the winter progressed, probably because of food depletion in shallow areas that permit higher intake rates (Guillemain and Fritz, 2002). In general, diving ducks feed more in offshore, deeper habitats than dabbling ducks (Pöysä, 1983a; Nudds, 1992).

4. Factors influencing selection and consumption of propagules by Anatidae

Though considerable work has been done on how the nutritional quality of leaves of various species influences foraging decisions by grazing Anatidae, much less has been done on the influence of nutritional quality on selection of seed types by waterfowl, but the evidence available suggests that this is important. Thus breeding white-faced whistling ducks (*Dendrocygna viduata*) and red-billed teal (*Anas erythrorhyncha*) fed mainly on terrestrial graminoid *Panicum schinzii* seeds which have a particularly high fat content, whereas ducklings of the former species fed mainly on *Amaranthus* seeds with a particularly high crude protein content as appropriate for growth (Petrie, 1996; Petrie and Rogers, 1996). However, ducks also consume poisonous castor beans in lethal doses (Jensen and Allen, 1981), suggesting that they have a limited capacity to assess nutritional quality of various seeds. Another factor favouring seed selection is the ease with which they can be digested (obviously this reduces dispersal potential; see also

Charalambidou and Santamaría, 2002). Such ease may explain the strong selection shown for water lily (Nymphaeaceae) seeds in several duck studies (Tréca, 1981a). Experiments suggest that seeds of *Nymphaea*, *Nuphar* and *Nymphoides* water lilies do not survive digestion by ducks or coots, though *Nymphoides peltata* seeds seem to be well adapted for external transport (Smits et al., 1989).

There is much less information about the factors determining the ingestion of animal propagules. Regrettably, almost no authors make a distinction between propagules and other animal tissues in diet studies. For example, while *Daphnia* ephippia are frequently consumed by many duck species, it is unclear to what extent they are consumed from the propagule bank in the sediments, or consumed while inside ephippial *Daphnia*. We expect both mechanisms to be important. Though *Daphnia* are mentioned in many studies of duck diet (e.g., Rogers and Korschgen, 1966; Swanson, 1977; DuBowy, 1997), no mention is made of the presence or the absence of ephippia (except for Sánchez et al., 2000). However, ephippial *Daphnia* were more likely to be consumed by red phalaropes (*Phalaropus fulicarius*) than non-ephippial *Daphnia* (Dodson and Egger, 1980), a positive selection also observed by fish predators (Mellors, 1975).

5. When are propagules likely to be carried by Anatidae?

Clausen et al. (2002) assume that submerged macrophyte seeds are consumed directly off the plant, yet ducks also consume seeds from the sediments favouring dispersal long after the seeds have been shed from the mother plant. Anatidae may rapidly deplete seeds when taken directly from the plants (e.g., *Salicornia* seeds, Van Eerden, 1984; Summers et al., 1993; Potamogeton seeds, Santamaria, unpubl.; Clausen et al., 2002), and the availability of such seeds may vary greatly from year to year (because of changes in the environmental conditions or relative abundance of various plant species). In comparison, availability of seeds from banks in the sediments is likely to be less variable between years (e.g., Bonis et al., 1995), though fluctuations in water depth have a major influence on their availability to dabbling ducks and waders (Pöysä, 1983b; Gray and Bolen, 1987; Ntiamoa-Baidu et al., 1998). Furthermore, depletion of seeds from banks in the sediments by Anatidae is slower and less efficient. Even in the shallow areas most used by feeding ducks, Gray and Bolen (1987) found only marginally significant seed bank depletion between September and April. In temporary marshes in the Camargue, France, Bonis et al. (1995) found no measurable depletion by birds. Thus there is likely to be less potential for seasonal and annual variation in dispersal of seeds consumed from sediments than from seed heads on the plant. However, in Doñana we have recorded a 53% reduction in the density of widgeongrass *Ruppia maritima*

seeds in sediments from September to May ($P = 0.007$) because of consumption by ducks, other waterbirds and potentially also fish. There is no consistent change between duck species in the area in the numbers of intact seeds defecated between autumn and spring (authors, unpublished), suggesting similar potential for southward and northward dispersal (contrary to Clausen et al., 2002).

In this section, we consider seasonal changes in dispersal potential by reviewing studies of Anatidae diet (mainly data on the contents of the gullet and gizzard). Our review is not totally comprehensive, especially given the enormous quantity of grey literature on waterfowl diet. It is very difficult to predict dispersal potential based on such diet studies for several reasons. First, the proportion of propagules surviving digestion is itself affected by changes in diet composition. Research in captivity suggests that seeds mixed with a mainly animal diet can survive digestion better than those incorporated in a purely seed diet (Charalambidou and Santamaría, 2002, I. Charalambidou, unpublished). We provide here a unique example of how seasonal differences in the consumption rates of various seeds are *not* reflected by a change in dispersal potential. *Ruppia* and *Salicornia* seeds were much more abundant in marbled teal (*Marmaronetta angustirostris*) diet at Sidi Moussa, Morocco in October than in May, whereas *Ranunculus* seeds were much more abundant in May (A.J. Green and M.I. Sánchez, unpublished). However, when the numbers of intact, apparently viable seeds found in faeces are compared, there is only a significant seasonal effect in the case of the *Ranunculus* seeds (Fig. 1). This illustrates how diet switches do not necessarily translate into changes in dispersal potential.

Furthermore, diet studies show that seeds of a given type are often present in small numbers but in a large proportion of the bird population (e.g., Cyperaceae seeds in garganey,

Anas querquedula, Tréca, 1981a), whereas seeds of other types are found in large numbers but only in a small number of birds (e.g., *Echinocloa* seeds in garganey, Tréca, 1981a). Without affecting the overall proportion of a given seed type in the diet of the bird population, these two distribution patterns have very different implications for dispersal. When a seed type is carried by more birds, there is more chance that one bird will move the seed a long distance to a suitable habitat. However, ingestion of the same seed in large quantities may increase survival of digestion in some situations (authors, unpublished). Tamisier (1971) commented that relatively more seeds survived digestion (i.e., remained intact in the rectum) by Eurasian teal as their overall ingestion rate increased.

Seasonal diet switches are inevitable in seasonal environments, and there is a tendency in migratory duck species in the northern hemisphere to feed relatively more on seeds rich in carbohydrates during the autumn and winter periods and relatively more on invertebrates during the breeding season and in the immediate postbreeding period when the flightless moult occurs (DuBow, 1988; Hohman et al., 1992; Krapu and Reinecke, 1992; Baldassarre and Bolen, 1994), but there are many exceptions to this, some of which are covered in the following review.

Though considerable information is available on seasonal differences in the importance of invertebrates in duck diets, we are only aware of one published study providing information on seasonal differences in the ingestion of invertebrate resting eggs. *Artemia* cysts were present in the faeces of shelduck wintering in the Camargue from October to February, being present in 20% (October) to 98% (December) of samples (Walmsley and Moser, 1981).

Sánchez et al. (2000) found cladoceran ephippia in the upper guts of 21 of 68 stiff-tails (*Oxyura* spp.) in Spain and they were present in birds sampled throughout the year with no clear seasonal trend (authors, unpublished). *Daphnia* ephippia were found in 42% of marbled teal faecal samples collected at Sidi Moussa, Morocco in October, and 32% of samples in May, a non-significant difference (A.J. Green and M.I. Sánchez, unpublished). Likewise, there was no seasonal change in the numbers of intact ephippia per sample (Fig. 1).

5.1. Studies of north-temperate ducks on migration

Despite the wealth of studies of migratory ducks in North America and Europe, relatively few studies have been made of the diet of ducks at passage sites. However, several studies give an insight into the relative potential for southward movements of propagules during autumn migration and northward movements during spring migration.

Aquatic seeds (from seven genera) were found in 82% of the gullets of buffleheads (*Bucephala albeola*) and lesser scaup on spring migration through California, USA, constituting 34% and 23% of aggregate volume, respectively

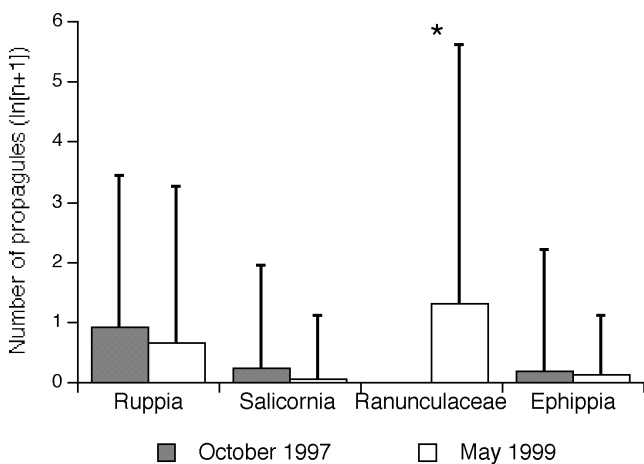


Fig. 1. Seasonal variation in the presence of propagules in faeces of marbled teal (*Marmaronetta angustirostris*) collected at Sidi Moussa-Oualidia in Morocco, showing means and range after transforming ($\log_e [n + 1]$), thus means are similar to geometric means) the numbers of intact seeds and ephippia per faecal sample. Ephippia were from *Daphnia* spp. The seasonal effect was only significant in the case of *Ranunculus* seeds (Mann–Whitney U -test; $n = 19, 28$; $U = 152$; $P < 0.002$).

(Gammonley and Heitmeyer, 1990). The most abundant seeds were *P. pectinatus* (45% of bufflehead gullets, 36% of scaup), *Scirpus robustus* (64% and 27%) and *Polygonum lapathifolium* (45% and 54%). These species are generally considered invertebrate specialists, yet their capacity for northward dispersal of seeds could be important. Lesser scaup on autumn migration through Illinois were consuming much less plant material, though *Potamogeton* and *Scirpus* seeds were present in 26–27% of gizzards (Rogers and Korschgen, 1966). In scaup migrating through northwestern Minnesota, seeds had a similar frequency in gullets in spring (eight genera, 42%) and autumn (five genera, 26% for immatures, 50% for adults), but *Potamogeton* seeds were more abundant in spring (21%) than in autumn (6% immatures, 14% adults; Afton et al., 1991).

Blue-winged teal (*Anas discors*) on spring migration through Missouri consumed seeds from 28 genera, totalling 35% of aggregate gullet mass and with 55–100% of gullets containing spike rush (*Eleocharis*) seeds and 55–70% containing floating primrose willow (*Ludwigia repens*), rice-cut grass (*Leersia oryzoides*) or *Panicum* grass seeds (Taylor, 1978). In California, 26% of aggregate gut content dry mass in unpaired male cinnamon teal *A. cyanoptera* on spring migration was made of seeds of 11 genera (including wideongrass; Hohman and Ankney, 1994). In New Mexico, oesophagi of females on spring migration contained 19% *Scirpus* and 4% *Polygonum* seeds (by aggregate dry mass), whereas immatures on autumn migration contained 25% *Scirpus*, 10% *Polygonum* and 40% *Echinochloa* (Gammonley, 1996).

The gullet contents of migratory mallards from Missouri during October–December were dominated by seeds of wild millet (*Echinochloa* spp.), nodding smartweed (*Polygonum lapathifolium*), rice-cut grass, arrowhead (*Sagittaria latifolia*) and Pennsylvania smartweed (*P. pennsylvanicum*) (Gruenhagen and Fredrickson, 1990). Apparently intact seeds were found in the large intestine or cloaca of 10 of 20 mallard, four of 10 green-winged teal (*Anas carolinensis*) and two of six blue-winged teal collected during October–November in Wisconsin (Montaba, 1971). Seeds included Pennsylvania smartweed, *Polygonum persicaria*, *P. punctatum*, *Scirpus validus*, *Potamogeton natans*, *Eleocharis elliptica* and rice-cut grass.

Pintail using vernal pools in California have been reported to feed on moist-soil seeds (mainly *Crypsis*, *Echinochloa*, *Polygonum* and *Eleocharis*) during both autumn and spring migration periods, but to feed on emergent seeds (mainly *Scirpus acutus* and *S. maritimus*) in midwinter (Silveira, 1998).

Gill (1974) suggested that ducks and geese internally disperse slough grass (*Beckmannia syzigachne*) seeds on both autumn and spring migration in Canada, but that spring migration is the most important in explaining its northerly distribution.

5.2. Studies of north-temperate ducks on wintering grounds

Many studies allow us to compare diet at a given wintering site during autumn/early winter and late winter/spring, when long-distance dispersal is most likely southwards and northwards, respectively. In the San Joaquin Valley, California, swamp timothy (*Heleochoa schoenoides*) seeds were present in 56% of northern pintail oesophagi sampled from September to November but only 15% of birds sampled from December to February, and curly dock (*Rumex crispus*) seeds decreased from 33% of birds to 9%. By contrast, the presence of nodding smartweed (*Polygonum lapathifolium*) seeds increased from 16% of birds to 28% (Connelly and Chesemore, 1980). In the Central Valley, California, swamp timothy and barnyardgrass (*Echinochloa crusgalli*) seeds became progressively less abundant in the oesophagi of pintails from October to February, but alkali bulrush (*Scirpus paludosus*) and sprangletop (*Leptochloa* spp.) seeds became progressively more important from December onwards. Seasonal trends for a given plant species were not so marked in the diet of green-winged teal collected in the same area, but overall seeds became progressively less important in the diets of both ducks as the winter proceeded (Euliss and Harris, 1987). Pintail and green-winged teal were reported to concentrate feeding on ammania (*Ammania coccinea*) and barnyardgrass seeds when they floated and concentrated on pond surfaces in early winter, though pintail later switched to feeding on barnyardgrass seeds concentrated on the pond bottoms (Euliss and Harris, 1987).

Consumption of water lily (*Nymphaea odorata*) seeds by ring-necked ducks (*Aythya collaris*) reduced from 29% of the total food dry weight in the gullet during October–December to 15% during January–March (Hoppe et al., 1986), though these seeds may not be able to survive digestion. By contrast, Jeske et al. (1993) found water lily seeds to be relatively less important in the diet of this species during November–December than during late winter.

In northern Europe, brent geese (*Branta bernicla*), Eurasian wigeon (*Anas penelope*) and other Anatidae feed extensively on *Salicornia europaea* seeds and leaves in autumn shortly after the seed crops ripen, and consume many fewer seeds in late winter (Van Eerden, 1984; Summers et al., 1993). Greylag geese (*Anser anser*) wintering in Doñana feed mainly on *Scirpus* tubers (Amat, 1995), but c. 20% of faeces contained intact *S. maritimus* seeds in January (authors, unpublished), a time when the geese regularly move hundreds of kilometres to alternative wintering sites (Nilsson et al., 1999). Giant Canada geese (*Branta canadensis maxima*) about to start spring migration in Minnesota were consuming some grass seeds of the millet tribe Paniceae (McLandress and Raveling, 1981).

In the Camargue, seeds were much more important in the diet of Eurasian coot during August–October (when they constituted 43% of prey items) than during November–

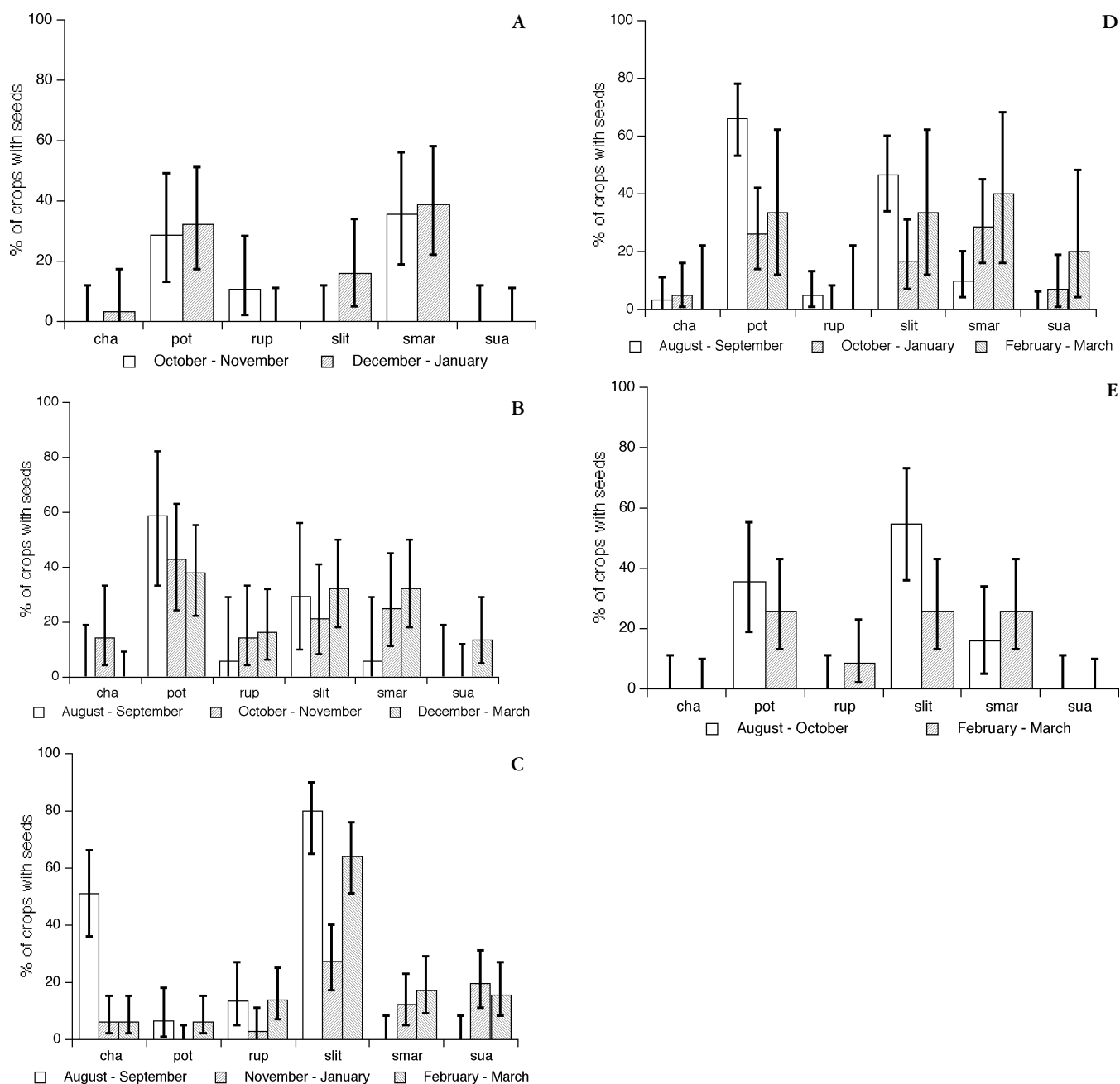


Fig. 2. Frequency of diaspores (i.e., percentage of individual ducks in which each seed or oospore type was recorded), in the crops of various duck species collected in the Camargue, France, at various times of the autumn and winter, showing 95% confidence intervals. A: northern pintail (*Anas acuta*) (n = 59), B: northern shoveller (*Anas clypeata*) (n = 82), C: Eurasian teal (*Anas crecca*) (n = 175), D: mallard (*Anas platyrhynchos*) (n = 119) and E: garganey (*Anas querquedula*) (n = 66). Diaspores shown are cha = *Chara* sp. (large size), pot = *Potamogeton pectinatus*, rup = *Ruppia maritima*, slit = *Scirpus litoralis*, smar = *Scirpus maritimus*, sua = *Suaeda maritima*. Data from [Pirrot \(1981\)](#) show only a selection of the most important diaspores in duck diets (with the permission of the author). Birds were collected from 1964 to 1966 and from 1979 to 1981; hence, there is a confounding year effect.

February (less than 8% of food items, Allouche and Tamisier, 1984). Major seasonal variations have been found in Eurasian teal (Tamisier, 1971) that consumed relatively large amounts of *Suaeda* seeds during November–January, and relatively large amounts of charophyte oospores and *Scirpus* seeds during August–October and also during February–March. [Pirrot \(1981\)](#) provides fascinating data on the

ingestion rates of various plant seeds by five different dabbling ducks at different stages of the autumn and winter period in the Camargue, one of Europe's most important wintering sites (Fig. 2).

These data refer to the proportions of birds carrying each seed type in their crops, and provide no information on the abundance of those present (shovellers fed principally on

invertebrates, whereas the other four species fed principally on seeds; see Tamisier and Dehorter, 1999 for quantitative data). In general, there are marked differences between duck species in the relative importance of various seeds (e.g., note the greater importance of *Chara* and *S. litoralis* and the lesser importance of *P. pectinatus* in the teal). Within species, there are significant differences between seasons in the importance of various seeds, but few seasonal trends are consistent between species. *Scirpus maritimus* is the seed showing the most marked trend, growing in frequency as the winter period goes on in all five species. In contrast, the closely related *S. litoralis* tends to be more abundant during August–September than during October–January (highly significant for teal and mallard).

M. Guillemain (unpublished) found that mallard and Eurasian teal wintering in western France began the winter by feeding on relatively large seeds at shallow depths (likely to provide higher rates of energetic intake), then increased their niche separation through the winter with mallard feeding on large seeds but at progressively greater depths, and teal remaining in shallow areas but switching to smaller seeds. However, this seasonal shift in seed size was not recorded in the Camargue (Fig. 2).

5.3. Studies of north-temperate ducks on breeding sites

Some studies allow us to compare diets at the beginning of the breeding season (when birds are still arriving and some continue on northward) with the end of the summer (when some birds are moving southwards on autumn migration, or potentially northwards on moult migration).

Blue-winged teal on breeding grounds in Saskatchewan fed on seeds from 13 genera, with *Sparganium* consumed mainly during May–June after arrival, *Scirpus* and *Nuphar* consumed mainly during August–September before leaving and *Eleocharis* and *Carex* important from May to September (Dirschl, 1969). Lesser scaup on breeding grounds in Saskatchewan fed on seeds from 11 genera, with *Nuphar* seeds being a major diet component during August–September just after they ripened and *Sparganium* consumed mainly during July–September (Dirschl, 1969).

5.4. Studies of ducks outside north-temperate regions

Outside the north-temperate climatic regions (where most research on Anatidae has been concentrated), there is by no means a general rule that ducks consume more invertebrates and fewer seeds during the breeding seasons. For example, Petrie and Rogers (1996) found breeding white-faced whistling ducks in South Africa to feed almost exclusively on seeds, especially the terrestrial graminoid *Panicum schinzii*, which is abundant in newly flooded ephemeral wetlands. In the same region, Petrie (1996) found red-billed teal feeding mainly on *P. schinzii* seeds during

both the breeding and postbreeding periods. Both duck species regularly consumed aquatic *Scirpus* and *Polygonum* seeds in small quantities during the breeding season. The diet of non-breeding white-faced whistling ducks (in a different part of South Africa) from early winter to spring was dominated by aquatic seeds, especially *Scirpus brachyceras* at one site and *Nymphaea* sp. and *Polygonum lapathifolium* at another, with no consistent trends as the season progressed (Petrie and Rogers, 1997a).

Tréca (1981a, b, 1986) provides a fascinating comparison of seasonal variation in the diets of the migratory garganey and the tropical white-faced and fulvous (*D. bicolor*) whistling ducks in the Senegal Delta. The whistling ducks are present in the delta all year round, but are capable of long-distance movements across Africa (Scott and Rose, 1996). As well as rice, all three species consumed diaspores of *Nymphaea*, Cyperaceae (*Scirpus* and *Picreus*), Gramineae (*Echinochloa colona* and *Panicum laetum*), Gentianaceae (*Limnanthemum senegalense*) and *Chara*. However, there were major differences between duck species; for example, garganey consumed much more Cyperaceae and *Chara*. Strong seasonal patterns were observed within each duck species, with garganey feeding relatively more on *Echinochloa* during October–November after arrival, on *Chara* in March before leaving, on Cyperaceae in December and February and on *Nymphaea* in January. In contrast, white-faced whistling ducks fed relatively more on *Echinochloa* from March to October, on *Limnanthemum* from November to December, on *Nymphaea* from November to March and on *Chara* in November and January. *D. bicolor* fed relatively more on *Echinochloa* from June to September, on *Limnanthemum* from January to April, on *Nymphaea* from September to February and on *Chara* in March.

In semi-arid and arid environments, various seed types are dominant in Anatidae diets during the wet and dry seasons, largely due to the differences in vegetation types between ephemeral and more permanent wetlands. In Australia (Marchant and Higgins, 1993), the wandering whistling duck (*D. arcuata*) feeds more on grass seeds in the wet season and more on *Nymphoides* and *Polygonum* seeds in the dry season. The magpie goose (*Anseranas semipalmata*) also feeds on grass seeds in the wet season and on sedge rhizomes in the dry season. For the grey teal (*Anas gracilis*) in coastal Queensland, Australia, seeds of both freshwater and brackish plants were more abundant in the wet season, with invertebrates more important in the dry season.

6. How far are propagules carried, and in which direction?

Clausen et al. (2002) review the speed and timing of long-distance movements by Anatidae. All waterbirds also make local movements (e.g., between feeding and roosting or nesting sites) throughout the annual cycle and can thus readily move propagules between various wetlands that are

nearby, but have separate catchments. Thus even such local movements can have a major role in the dispersal of aquatic organisms that cannot move between catchments via flotation, fish or other means. Ducks and geese often fly tens of kilometres between feeding and roosting sites (see, e.g., Tamisier and Dehorter, 1999, for movements of wintering ducks and coots within the Camargue). Wintering ducks in western France (Guillemain et al., 2002) and elsewhere disperse locally at night. In addition, northern migratory ducks rarely remain in the same area for several months once they reach a wintering site. Many species show high mobility during the winter, making regular movements between various wetlands (Pradel et al., 1997), partly in response to cold weather (Ridgill and Fox, 1990). In Mediterranean and semi-arid regions, bird concentrations regularly shift location by tens or hundreds of kilometres at any time of the year in response to rainfall. As an extreme example of foraging movements, flamingos breeding at Fuente de Piedra, Spain, fly up to 360 km to feed at various wetlands before returning to feed their chicks (Amat et al., 2001).

Long-distance movements of propagules are not only confined to those waterbird species with cyclical and predictable north–south migrations to and from more extreme latitudes. Many species show long-distance nomadic movements in response to the flooding and drought cycles of temporary wetlands in arid and semi-arid environments (Kingsford and Porter, 1993; Simmons et al., 1998; Kingsford et al., 1999). Among classic migratory species, there are great differences between species and even between populations in migratory behaviour. Thus, among western Palaearctic ducks, pintail and garganey make particularly long movements, whereas mallards are particularly sedentary but with great variation between and within mallard populations (del Hoyo et al., 1992; Scott and Rose, 1996). As well as long-distance movements between breeding and wintering grounds, many migratory Anatidae species make long movements upon completing breeding to sites more suitable for the flightless moult completed before winter migration begins (Hohman et al., 1992; see Clausen et al., 2002).

An extreme case of nomadic long-distance movements is shown by pink-eared duck (*Malacorhynchos membrana-ceus*) (Kingsford, 1996), which feeds principally on invertebrates but also on seeds (Marchant and Higgins, 1993). Sizeable flocks of over 1000 ducks were seldom recorded at the same wetland more than once in a 12-year period of annual surveys. Such nomadic dispersal patterns between ephemeral wetlands may have major effects on the genetic structure of dispersed plants and animals, but would be much harder to demonstrate than the effects of a directional north–south migration pattern, as there are no defined flyways.

Major switches in habitat use are usually associated with long-distance movements by waterbirds, and Clausen et al. (2002) discuss how this can hinder dispersal. Ducks show a

tendency to winter on larger, more open wetlands and breed on smaller wetlands with more luxuriant vegetation, though the details are species-specific. Heitmeyer and Vohs (1984) found major differences in the way eight dabbling duck species distributed on small wetlands of different types (lakes, rivers, open and vegetated marshes) while on migration through Oklahoma. Seasonal differences were also found within species; for example, green-winged teal selected lakes in autumn, but marshes in spring. However, great spatial and temporal variation is often found in habitat use for a given waterbird species. Even when a duck undergoes a major shift in wetland size or maximum depth after a migration journey, there are often plant or invertebrate species that can survive in both sites (especially around the shoreline) and be dispersed between them.

At intermediate latitudes, classical migratory duck species overlap with other species with greater nomadic tendencies and each group may disperse propagules in different directions. For example, marbled teal (which shows both migratory and nomadic tendencies) in Spain often move northeast in late summer/autumn (Navarro and Robledano, 1995) when classical migratory species breeding further north are moving in the opposite direction (Navarro and Robledano, 1995; Green and Navarro, 1997). Diet studies (A.J. Green and M.I. Sánchez, unpublished) and captive experiments (Figueroa and Green, 2002b) strongly suggest that marbled teal internally transport viable *Ruppia* and *Scirpus* seeds between suitable habitats during these northerly movements.

Throughout the world, the creation of reservoirs and other artificial wetlands has led to major changes in migratory movements of waterbirds (e.g. Švažas et al., 2001) with consequent implications for dispersal that are yet to be understood. In South Africa, Petrie and Rogers (1997b) suggest that the creation of irrigation ponds has caused whistling ducks “to winter close to breeding areas and be more fixed and predictable in their annual movements (i.e., more migratory and less nomadic, dispersive, facultative”).

Waterfowl undergo high mortality rates during the winter period (Baldassarre and Bolen, 1994; Kremetz et al., 1997) and the numbers of waterfowl migrating south are much higher than those returning north. This factor will tend to make long-distance dispersal more frequent southwards than northwards.

7. Conclusions

The literature on waterbird ecology suggests that Anatidae, shorebirds and other waterbirds have an important role in the population and community ecology of aquatic invertebrates and plants by acting as vectors of passive dispersal. Our review confirms that Anatidae and shorebirds have great potential as dispersers of aquatic organisms, but shows that there are certainly to be great differences

between closely related, sympatric bird species in their roles in dispersal of specific aquatic organisms. Furthermore, there is likely to be great spatial and temporal variation (i.e., a great deal of noise) in dispersal patterns realized by a given bird population.

Though seed consumption by north-temperate ducks is generally higher during the migration and wintering periods than during the breeding season, the above review shows that the seasonal patterns recorded in autumn and spring or in early and late winter are not consistent. In a given study, some seeds are consumed more during autumn or early winter and others are consumed more during late winter or spring. These patterns also show major variation between study sites and probably also years, as has been described in bird-mediated dispersal within terrestrial ecosystems (Herrera, 1998).

Though many duck species have quite marked migratory patterns, long-distance movements of propagules by them are likely to be highly unpredictable. The consumption and adhesion of propagules by and to ducks is certain to be subject to great temporal and spatial variation, even within a given wetland complex, in relation to changes in the distribution of propagules and of birds, water depth fluctuations (which change the availability of propagules in the sediments, especially to dabbling ducks) and changes in the availability of other food items (invertebrates, agricultural waste grain, etc.). The survival by propagules of digestion is also certain to fluctuate enormously (Figuerola and Green, 2002a; Charalambidou and Santamaría, 2002), making it difficult to draw conclusions from diet studies reviewed above in which the state of propagules after digestion is not addressed.

Previous authors have usually focused on the bird species without paying attention to their role as dispersers, and there is relatively little detailed information from field studies that allows us to identify patterns in dispersal. Much more fieldwork or reanalysis of the existing data sets (e.g., more detailed analysis of gut contents) is needed before the relative importance of different waterbird species in the dispersal of specific plants or invertebrates can be accurately assessed, or before any seasonal trends in dispersal can be firmly established.

In the few studies allowing seasonal diet comparisons, they are confounded by year effects (i.e., birds are collected over different years, then combined). There is an acute lack of studies comparing diet at the same site over different parts of the same annual cycle (e.g., autumn with the following spring). Thus, the observed seasonal patterns reported above may be strongly biased by differences between years (in seed production, water levels, etc.). There is a particular need for studies of faecal contents that compare the number of viable propagules defecated by birds at a given location at different parts of a single annual cycle (especially comparing autumn and spring migration periods). Faecal analysis has rarely been used to study duck diet (Green and Selva, 2000), largely owing to the difficulty in

assessing the relative proportions of various items at ingestion, yet this method is much more suitable for studies of dispersal capacity than for studies of gut contents. There is an urgent need for more work about how and when waterbirds ingest invertebrate propagules, and particularly on spatial and temporal variation in external transport of both plant and animal propagules (about which we have said little owing to the acute shortage of available data).

The relative importance of moult migration, winter movements and autumn/spring migration in long-distance dispersal of plants and invertebrates is currently open to speculation and is one of many subjects for future research. We suggest that Clausen et al. (2002) underestimate the potential for dispersal of seeds northwards in temperate environments, especially owing to the consumption of seeds from sediments. We have cited several studies documenting consumption of *Potamogeton* and *Ruppia* seeds by ducks on spring migration or in late winter. Our own unpublished data demonstrate high rates of consumption of widgeongrass *R. maritima* seeds by spring migrants in Doñana, as well as defecation of viable seeds. The data we have presented on marbled teal (Fig. 1) show that consumption and dispersal of *Ruppia* seeds are not restricted to the late summer/autumn period when seeds are produced.

We encourage waterbird biologists to make a contribution to furthering understanding of dispersal processes by using birds captured or collected for other studies. Studies conceived to address an aspect of the ecology of bird species could often be easily adapted to address the role of that bird in the wider aquatic community. For example, conventional diet studies can be easily extended to record data on the presence and state (i.e., intact or not) of invertebrate and plant propagules. The screening of birds captured for ringing programmes for externally attached propagules is straightforward and would provide invaluable information about external transport, which could be integrated with the ringing recovery data to assess the directionality of dispersal. Birds collected for diet studies could also be inspected externally for propagules and the inspection of lower gut as well as upper gut contents would clarify which propagules apparently survive ingestion intact, complementing information on ingestion. Where birds are not collected, faeces samples could often be taken and the viability of propagules could be assessed (e.g. birds often defecate when collected for ringing).

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