CHAPTER SIX

Dispersal of Plants by Waterbirds

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The widespread distribution of fresh-water plants and of the lower animals, whether retaining the same identical form or in some degree modified, I believe mainly depends on the wide dispersal of their seeds and eggs by animals, more especially by fresh-water birds, which have large powers of flight, and naturally travel from one to another and often distant piece of water. —Charles Darwin (1859)

Humans have had a long and special relationship with waterbirds, particularly as sources of food both in the wild and following domestication (Kear 1990; Green and Elmberg 2014). Today waterbirds remain a great attraction as hunting quarry, and tens of millions of dollars are spent each year by waterfowl hunters in North America alone. Bird watchers and other people visiting nature reserves often search out the major spectacle provided by waterbirds on migration or on their wintering grounds. Management for hunting or conservation interests often focuses on the measures that attract the largest concentrations or diversity of migratory waterbirds. However, managers usually pay little or no attention to the vital role of birds as dispersers of plants and invertebrates that lack their own active means of dispersal, but which can be transported over great distances on the outside or inside of waterbirds.

The dispersal of viable plant units (hereafter "diaspores") may be the most important ecosystem service provided by birds (Şekercioğlu 2006). However, the great majority of diaspore dispersal literature focuses on the dispersal of plants with fleshy fruits by terrestrial birds (chapter 5). Nevertheless, ducks, shorebirds, and other waterbirds play major roles as vectors of passive dispersal for plants, both by internal transport within their guts ("endozoochory"; e.g., see Figuerola and Green 2002a; van Leeuwen

FIGURE 6.1. Eurasian coot (*Fulica atra*) with duckweed (*Lemna gibba* or *L. minor*) attached to its bill. Photo by Nicky Petkov / www.NaturePhotos.eu.

et al. 2012) and by external transport on feathers or skin ("epizoochory" or "ectozoochory"; e.g., see Figuerola and Green 2002b; Brochet et al. 2010a; fig. 6.1). As shown experimentally by Darwin (1859), secondary internal transport can also occur, when diaspores are first ingested by fish or crustaceans that are then predated by piscivorous birds. In addition, plants may be dispersed when waterbirds use them as nest material. Many of the plants dispersed by waterbirds are major components of ecosystems, and provide numerous indirect benefits to humans.

Dispersal is crucial for the regional survival, range expansion, and migration of plant species, especially plants that are confined to spatially discrete habitats in an otherwise unsuitable landscape (Howe and Smallwood 1982). Nonmarine aquatic or wetland habitats are often islandlike in their spatial isolation from one another. Dispersal processes to islands and to inland waterbodies, such as lakes or ponds, are cases in which metapopulation or metacommunity models apply to plant populations (whether island, or aquatic, or both). In both island and island-like aquatic systems, waterbirds are important vectors of passive dispersal for numerous plant species. They are highly mobile on short and long timescales, including frequent daily movements and seasonal long-distance migrations. They are thus particularly good vectors for long-distance dispersal and maintain connectivity between plant populations in different catchments that

have no active means of interchange (Amezaga et al. 2002). Their importance as vectors is even greater today, as plants and other organisms need to move to adapt to the rapid changes to natural environments caused by human activity, including climate change. Suitable habitats for plant species change distribution continuously (e.g. as temporary wetlands dry and reflood, as some wetlands are degraded whilst others are created, or as the distribution of the suitable temperature range changes), and waterbirds provide a means by which plant species can track these changes.

Although waterbirds sometimes feed on fleshy fruits and disperse the seeds within, they mainly disperse wetland and terrestrial plants that lack fleshy fruits. Most plant species have what van der Pijl (1972) called "non-adapted diaspores" because they lack a fleshy-fruit and a priori are not obviously adapted for internal transport, while at the same time lacking hooks, barbs, or other apparent adaptations for external transport. Plant families lacking fleshy fruits have often been wrongly assumed to be exclusively dispersed by abiotic means such as wind or water, and for that reason many reviews of "zoochory" or biotic dispersal make no mention of waterbirds as vectors of diaspores (e.g. Tiffney 2004). Like interactions between herbaceous diaspores and large mammals (Janzen 1984), the study of interactions between plants and waterbirds has been rather unfashionable compared with interactions between vertebrates and forest plants with fleshy fruits. This is ironic, since Darwin (1859) paid more attention to the role of waterbirds as dispersal vectors than to the role of frugivores.

Diaspore dispersal by waterbirds is an ancient process that likely dates to the origin of waterbirds in the Early Cretaceous, coinciding with the origin and early radiation of the angiosperms (Soltis et al. 2008; Lockley et al. 2012). Darwin (1859) first drew attention to diaspore dispersal by waterbirds. He realized that their capacity as vectors of passive dispersal, coupled with their frequent and long-distance movements, provided an explanation over evolutionary timescales for the widespread distributions of many aquatic organisms, despite their own limitations for movement. Most of the literature exploring the dispersal of diaspores by waterbirds in detail focuses on aquatic plants. The truly aquatic plants (e.g., pondweeds) have no capacity for wind dispersal (anemochory, van der Pijl 1972), and this increases their dependency on dispersal by animals (zoochory) and water (hydrochory). However, dispersal by water is always limited to areas connected by surface water flows and thus cannot result in dispersal to isolated water bodies or wetlands in different catchments. Waterbirds also disperse diaspores of a variety of terrestrial plants, especially those from moist soils and those whose diaspores end up

being washed or blown into wetlands. The boundaries between "aquatic" and "terrestrial" are not rigid or clear-cut, since many important habitats are dynamic and are inundated only for part of the time and most waterbirds are not entirely aquatic. Furthermore, some aquatic plants can often tolerate a short terrestrial phase, and vice versa. Dormant diaspores can remain in seed banks until favorable conditions (whether wetter or drier) arise. Diaspore dispersal by waterbirds may be relatively unimportant in closed forests, but forests cover only 31% of total land area (http://www.fao.org/forestry/28808/en/). Furthermore, forest streams are often frequented by herons, kingfishers or specialized ducks, all of which may have an important role as vectors of dispersal upstream or between catchments. Wetlands cover an estimated 12% of land area (Downing 2009), but their catchment areas are far more extensive.

This chapter focuses on current understanding of plant dispersal by waterbirds. We begin with a review of principal waterbird families and their importance as plant vectors. We then review current understanding of the importance of zoochory for the ecology of plants, effects on seeds of gut passage through the waterbird gut, the plants that are dispersed, and the extent to which seed morphology can predict waterbird dispersal. We next consider the coupling of seed dispersal with seed production, the role of plant-waterbird coevolution, and the seed adaptations that exist for waterbird dispersal. We then focus on establishment success of dispersed diaspores. We conclude by considering how all this dispersal provides benefits to humans.

Waterbirds That Are Diaspore Vectors

No systematic surveys compare the relative importance of all waterbirds in a given region as vectors, and this makes generalizations about the roles of different bird groups difficult. All species can be expected to have some role in external and internal diaspore dispersal. Many waterbirds are dietary generalists. Many species of herons, spoonbills, cormorants, grebes, or terns concentrate on fish, although most of these birds also eat amphibians, reptiles, and large invertebrates such as crayfish. These waterbirds have major potential for secondary dispersal of plant diaspores ingested by their prey. Other waterbirds, such as storks, ibis, ducks, rails, gulls, and shorebirds, are typically omnivorous, eating a range of animals and plant material and varying their diets with age, season, or geographic location. Some birds, such as geese, wigeon, swans, and rallids (e.g. coots or

swamphens), are largely herbivorous but also ingest and disperse dia-
spores. The same is true of shorebirds and flamingos, which are often as-
sumed to be invertebrate predators.

Factors determining the importance of different waterbird species as
vectors include their abundance and degree of migratory behavior, both
of which are relatively well studied. In terms of numbers of species, popu-
lations and individuals, the Anatidae, shorebirds, Rallidae, and Laridae
(gulls and terns) are the most important waterbird groups, followed by
Ardeidae (herons and egrets; Wetlands International 2012; see fig. 6.2),
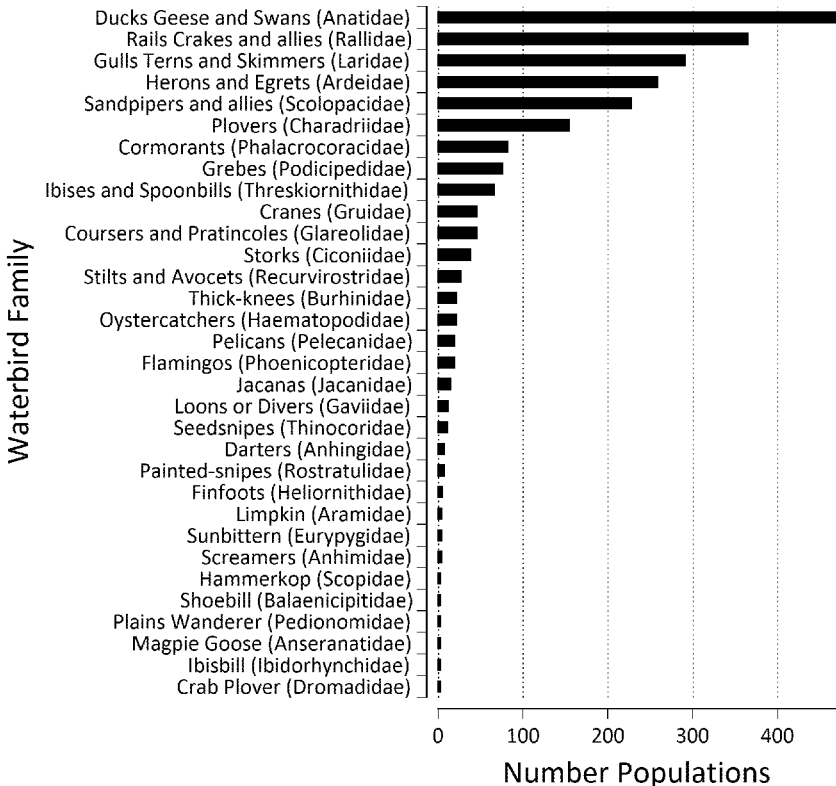and each of these groups is considered separately below.

FIGURE 6.2. Overview of bird families included in the term "waterbirds" as applied in this
chapter, with the global number of waterbird populations per family (from Wetlands Inter-
national 2012; details of population size for each population are available online at wpe.wet
lands.org).

Anatidae

Ridley (1930) provided extensive lists of plants whose seeds have been found in the guts of many waterfowl, especially Holarctic ducks. He found Cyperaceae particularly dependent on dispersal by ducks, and this is supported by recent literature. Migratory Anatidae are tremendously important diaspore dispersers in the Northern Hemisphere. Continental North America alone supports an estimated 49 million ducks, more than 10 million geese, and around 200,000 swans (USFWS 2012).

Pioneering research by Proctor and coworkers (Proctor 1968; deVlaming and Proctor 1968) has stimulated detailed, systematic, and quantitative studies on seed dispersal by waterbirds, but the great majority have focused on *Anas* ducks, for several reasons. First, *Anas* species are widespread and abundant, rendering them obvious candidates for study. Second, their ecology is well known, owing largely to their importance as hunting quarry, and diet studies have long since established that *Anas* species feed, often to a large extent, on plant seeds. Third, they are easily kept in captivity and legally hunted in large numbers, making them readily available as study objects both pre- and postmortem. For these reasons, most of the examples and analyses further on in this chapter are based on Holarctic *Anas* ducks. Hence, in this section we concentrate on the literature on other Anatidae species.

Investigations of the Pacific black duck (*Anas superciliosa*), grey teal (*Anas gracilis*), and chestnut teal (*Anas castanea*; Green et al. 2008; Raulings et al. 2011) of Australia confirm that both nomadic and seasonal migrant ducks are important endo- and epizoochorous seed vectors. In the Mediterranean region, the nomadic and globally threatened marbled teal (*Marmaronetta angustirostris*; subfamily Aythyinae) is also an important vector (Green et al. 2002; Fuentes et al. 2005). Amongst fish-eating migrants from the Merginae subfamily, red-breasted mergansers (*Mergus serrator*) and buffleheads (*Bucephala albeola*) were shown to carry seeds externally in New Jersey (Vivian-Smith and Stiles 1994).

The true geese (subfamily Anserinae) are more terrestrial than ducks, and in some cases are important for dispersal of plants with fleshy fruits. The endemic and globally threatened Hawaiian goose (*Branta sandvicensis*) disperses berries such as *Coprosma erno-deoides* (Rubiaceae), *Vaccinium reticulatum*, *Styphelia tameiameiae* (Ericaceae), and the Chilean strawberry (*Fragaria chilensis*; Rosaceae), as well as seeds of the alien sow thistle (*Sonchus asper* [Asteraceae]; Guppy 1906). Black et al. (1994) analyzed the feces of this goose and found four kinds of berries (mainly

S. tamaiameiae and *V. reticulatum*) and five types of grass seeds, especially molasses grass (*Melinis minutiflora*). Ridley (1930) reported how snow geese (*Anser hyperboreus*) consumed *Empetrum nigrum* (Ericaceae) berries and *Potamogeton natans* seeds, and greylag geese (*Anser anser*) consumed *Rubus chamaemorus* (Rosaceae) berries.

Geese grazing on grasses and other green plant material often ingest diaspores and disperse them in their feces in a manner analogous to that of herbivorous mammals which ingest seeds along with foliage (Janzen 1984). Barnacle geese (*Branta leucopsis*) are important for endozoochory in Arctic tundra (Bruun et al. 2008) and the Netherlands (Chang et al. 2005), while Canada geese (*B. canadensis*) are vectors of a range of native plants (Morton and Hogg 1989; Neff and Baldwin 2005) and alien grasses (Isaac-Renton et al. 2010). Viable seeds of *Scirpus maritimus*, *S. litoralis* (in Spain: A. J. Green and J. Figuerola, unpublished) have been recorded in the feces of migratory greylags. Seeds of smooth cordgrass (*Spartina alterniflora*), seashore saltgrass (*Distichlis spicata*), and seven other species were found on feet and feathers of brant geese (*Branta bernicla*) in New Jersey (Vivian-Smith and Stiles 1994). Brant geese in Europe feed on *Salicornia europaea* seeds (Summers et al. 1993).

Relatively little is known about diaspore dispersal by true swans (subfamily Anserinae), which may be more important vectors of aquatic plants than geese. Ridley (1930) reported that both mute swans (*Cygnus olor*) and Bewick's swan (*C. columbianus*) consumed *P. natans* seeds. Feces from black swans (*Cygnus atratus*) in Australia contained viable seeds of *Typha* and alien *Medicago* and *Polygonum* (Green et al. 2008).

Other groups of Anatidae are likely important diaspore vectors. Ridley (1930) proposed that whistling ducks (Dendrocygninae) are good vectors, as they ingest many aquatic plant species and range widely in areas like the Caribbean and Indonesia. The high proportion and variety of seeds in the diet of African and Australian *Dendrocygna* (Green et al. 2002) supports this. In South Africa, the spur-winged goose (*Plectropterus gambensis* [Plectropterinae]) ingests a variety of seeds (Halse 1985). The aberrant magpie goose (*Anseranas semipalmata*; often placed in its own family, the Anseranatidae) feeds partly on grass, *Polygonum*, and other seeds (Marchant and Higgins 1990).

Within the Tadorninae (shelduck subfamily), Ridley (1930) reported that the upland goose (*Chloephaga picta*) consumed berries of *Empetrum rubrum* in the Falkland Islands. In Tierra del Fuego, this species and the ashy-headed goose (*C. poliocephala*) are important frugivores (Willson et al. 1997). The shelduck (*Tadorna tadorna*) is a likely vector for *Salicornia*

seeds (Viain et al. 2011). In South Africa, the Egyptian goose (*Alopochen aegyptiacus*) is likely to be an important seed vector (Halse 1984). Fossilized feces of the extinct, flightless *Thambetochen chauliodous* from Hawaii, the size of a large swan but more related to shelducks or dabbling ducks, were rich in fern spores (James & Burney 1997).

Rallidae

Eurasian coot (*Fulica atra*; fig. 6.1) are similar to sympatric ducks in their internal dispersal of diaspores, with *Chara* in feces in France (Charalambidou and Santamaria 2005), viable *Ruppia* and *Arthrocnemum* seeds in Spain (Figuerola et al. 2002, 2003), and viable *Typha* seeds in Australia (Green et al. 2008). Diaspores of at least 13 species were present in their upper gut in northeast France (Mouronval et al. 2007), and 13 species in the Camargue, where coot consumed more seeds than gadwall (*Anas strepera*; Allouche and Tamisier 1984). Various saltmarsh seeds have been recorded on the feet and plumage of coot in Spain (Figuerola and Green 2002b), and Cook (1990) proposed that the seeds of the water lily (*Nymphoides peltata*) are dispersed when stuck on the bill or shield of coot.

Common gallinules (*Gallinula galeata*) in Argentina consumed seeds throughout the annual cycle, especially Polygonaceae and Poaceae (Beltzer et al. 1991). Sticky seeds of *Pisonia grandis* were recorded attached to six common moorhens (*Gallinula chloropus*) in the Seychelles, as well as to several seabird species (Burger 2005). Ridley (1930) reported that the water rail (*Rallus aquaticus*) takes *Rosa* and grass seeds, while the buff-banded rail (*Hypotaenidia philippensis*) eats fruits of *Freycinetia banskii* in New Zealand. Rails of the genus *Porphyrio* are major vectors of the genus *Coprosma* (Rubiaceae) within and between New Zealand and Pacific islands, and *Scleria* seeds (Cyperaceae) were in the gut of *Porphyrio* in Fiji (Guppy 1906). A seed of the Japanese chaff flower (*Achyranthes japonica*) was found in the feathers of a Swinhoe's rail (*Coturnicops exquisitus*; Choi et al. 2010). Seeds, especially *Caperonia palustris* (Euphorbiacea), *Thalia geniculata* (Marantaceae), *Eleocharis* (Cyperaceae), *Ludwigia* (Onagraceae) and *Neptunia oleraceae* (Fabaceae), are major food items of the purple gallinule (*Porphyrio martinincus*) in Venezuela (Tárano et al. 1995). Viable seeds of four *Eleocharis* species were recovered from feces of purple swamphen (*P. porphyrio*) in Australia (Bell 2000). Seeds of Typhaceae (*Sparganium ramosum*) and Cyperaceae (*Scirpus* spp. and *Carex divisa*) are a major part of the diet of this species in Spain (Rodríguez and Hiraldo 1975).

Shorebirds

The shorebirds (or "waders" as they are often called in Europe, not to be confused with "wading birds" in the North American sense) are a group of waterbird families with a similar morphology and ecology, within the order Charadriiformes. With migrations often across seas and oceans, their potential importance in diaspore dispersal to oceanic islands has long been recognized. Ridley (1930) reported internal transport of berry seeds by shorebirds, referring to the consumption of *Vaccinium* and *Empetrum* berries by Eurasian curlew (*Numenius arquata*) and *Pluvialis* plovers, and of *Canthium* fruits by bristle-thighed curlew (*N. tahitensis*) in Pacific islands. De Vlaming and Proctor (1968) were the first to demonstrate that Charadriidae shorebirds disperse angiosperms lacking fleshy fruits by internal transport. Proctor (1968) found experimentally that viable seeds that were regurgitated after being retained in the shorebird gizzard for up to 340 hours in killdeer (*Charadrius vociferus*) and 216 hours in least sandpiper (*Calidris minutilla*) remain viable. Proctor (1968) also observed that shorebirds reingest seeds regurgitated by individuals of other species. A given seed may thus be transferred between species and dispersed to and from microhabitats used by different species (e.g., terrestrial habitats). This seed transfer among different species may facilitate effective long-distance dispersal of diaspores. The extraordinary nonstop flights of bar-tailed godwits (*Limosa lapponica*) of over 8,000 km across the Pacific (Gill et al. 2009) underline their potential for long-distance dispersal.

Most shorebirds include seeds in their diet, including 37 of 55 shorebird species in the Western Palaearctic and 26 of 35 species in North America (Green et al. 2002). Seeds of at least 122 genera from 48 families have been recorded in the guts of common snipe (*Gallinago gallinago*; Mueller 1999). Seeds can be the most important food item for various species at certain times of the year, even at stoppage sites during spring and autumn migration (Green et al. 2002). On wintering grounds in Argentina, seeds from at least eight plant families were the only food items recorded for white-rumped sandpiper (*Calidris fuscicollis*; Montalti et al. 2003). External transport by shorebirds is also important but largely unstudied. Darwin (1872) germinated a seed of toad rush (*Juncus bufonius*) removed from mud attached to the leg of a Eurasian woodcock, *Scolopax rusticola*. Bryophyte and algal diaspores were recovered from the plumage of American goldenplover (*Pluvialis dominica*), semipalmated sandipiper (*Calidris pusilla*), and red phalarope (*Phalaropus fulicarius*; Lewis et al. 2014).

Sánchez et al. (2006) examined seed viability following passage through shorebird guts in the field. Viable seeds of *Mesembryanthemum nodiflorum* (Aizoaceae), *Sonchus oleraceus* (Asteraceae) and *Arthrocnemum macrostachyum* (Chenopodiaceae) were frequent in pellets and feces of common redshank, spotted redshank (*Tringa erythropus*), and black-tailed godwit (*Limosa limosa*) during spring and autumn migrations in Spain (Sánchez et al. 2006). Another 11 seed types were recorded at low densities.

Gulls

Calvino-Cancela (2011) reviewed internal transport by gulls. Berries are a major part of the diet of many species, and dispersal of fleshy-fruited plants by gulls greatly influences the development of oceanic island plant communities. However, seeds of plants lacking a fleshy fruit, common in grasslands and cultivated fields, are also dispersed. Seeds have been recorded in the diet of at least 22 gull species, mainly those using inland freshwater habitats. Gulls are not efficient at digesting seeds, and often regurgitate or defecate them intact. Plants dispersed include many genera frequent in duck diets, such as *Polygonum*, *Plantago*, *Chenopodium*, *Rumex*, *Carex* and *Scirpus*. Retention times can exceed 70 hours for defecated seeds and 45 hours for regurgitated seeds, and viability has been demonstrated in several studies. On Surtsey, a volcanic island that appeared in 1963, gulls have brought most of the soil nitrogen, as well as most of the plants (Magnússon et al. 2009).

Gulls help spread alien weeds from agricultural land and garbage dumps to islands. Morton and Hogg (1989) recovered seeds of 23 plant species in pellets and feces of ring-billed gull (*Larus delawarensis*) and herring gull (*L. argentatus*) on an island in Lake Huron. Seeds of nineteen species later germinated. Most (18) of these plant species were exotics (e.g., *Poa annua*, *Chenopodium album*, *Amaranthus retroflexus* and *Taraxacum officinale*) that dominated vegetation around the nesting sites. They also found that herring gull nests contained 15 plant species (only two of which were present in pellets and feces) with viable rootstocks, rhizomes, or seeds.

Earthworms, which themselves ingest and disperse diaspores (Milcu et al. 2006), are common in gull diets (Calvino-Cancela 2011). Gulls may indirectly disperse diaspores within the earthworms they consume.

Herons

Grey heron (*Ardea cinerea*) pellets in Tenerife contained seeds of at least 16 plant species ingested by lizards which are preyed on by the herons,

facilitating secondary dispersal of terrestrial plants, although to a lesser extent than by kestrels and shrikes (Rodríguez et al. 2007). Heslop-Harrison (1955) reported viable seeds of *Nuphar lutea* (presumed to have been eaten by a fish) in excreta from a grey heron. Corlett (1998) reported that cattle egrets (*Bubulcus ibis*) eat figs. Seeds of *Achyranthes japonica* were found in the feathers of a Eurasian bittern (*Botaurus stellaris*; Choi et al. 2010).

Other Waterbirds

Arber (1920) reported that Weddell (1849; predating Darwin 1859) observed a tiny, previously unknown floating plant on the feathers of a waterbird in Brazil (a "camichi," a local name for a horned screamer [*Palamedea cornuta*], according to Maximilian 1820). Weddell described this new species as *Wolffia brasiliensis*. Greater flamingos (*Phoenicopterus roseus*) often filter food items from the sediments, and ingest *Ruppia maritima* seeds (Rodríguez-Pérez and Green 2006) and presumably many other diaspores. Holmboe (1900) reported that common cranes (*Grus grus*) consumed *Vaccinium vitis-idea* berries. Australian pelican (*Pelecanus conspicillatus*) feces contained viable diaspores of *Lemna*, *Nitella* and *Typha*, which were presumably first ingested by fish (Green et al. 2008). Ridley (1930) reported occasional seeds in the stomachs of grebes.

Ridley (1930) reported the presence of berries in the diets of skuas, and occasional seeds in petrels. Aoyama et al. (2012) quantified external transport of nine plant species by four species of seabird: the black-footed albatross (*Phoebastria nigripes*), Bulwer's petrel (*Bulweria bulwerii*), wedge-tailed shearwater (*Puffinus pacificus*), and brown booby (*Sula leucogaster*). Carlquist (1967) observed sticky *Boerhavia diffusa* fruits on the feathers of the sooty tern (*Onychoprion fuscatus*).Taylor (1954) and Falla (1960) suggested that various plants reached oceanic islands through external transport on albatrosses and petrels.

The Significance of Passive Dispersal by Waterbirds for Wetland Plant Species

Wetlands often occur spatially scattered throughout otherwise dry (or drier) terrestrial landscapes, so that wetland habitat exists in the form of discrete and isolated patches in an otherwise unsuitable landscape. Human land development has reduced wetland area and increased wetland fragmentation globally, exacerbating the isolation of remaining wetland areas

(Davidson 2014). Loss of connectivity between isolated wetlands and associated changes in land use may result in local and regional species extinctions, loss of regional species dynamics, and increased vulnerability of remnant populations to stresses such as pollution or climate change (Amezaga et al. 2002; Lougheed et al. 2008; Wormworth and Şekercioğlu 2011). Even under natural conditions, plant species must disperse across the landscape to reach new wetland habitats in order to escape from predators, pests, and pathogens and to reach new unoccupied sites to balance the loss of occupied sites. Hence, for the preservation of wetland plant diversity and wetland functions provided by the plant species, dispersal among wetlands is crucial.

Five main dispersal mechanisms have the potential to connect isolated wetlands: wind, water, birds, humans, and other animals. Dispersal by wind is uncommon in submerged or floating plants, as they mostly produce diaspores under or in the water. Many plants (most notably the tall *Epilobium*, *Typha*, and *Phragmites* species and trees such as *Salix*, *Alnus*, and *Betula*) produce seeds in and around wetlands that are well dispersed by wind over distances exceeding tens of kilometers, but the direction of the wind is unpredictable and many seeds are lost (Soons 2006). Hydrochory of diaspores produced under, in, or near the water surface transports diaspores between wet areas likely to offer suitable habitat (Sarneel et al. 2013; Soomers et al. 2013). However, water flows transport diaspores only downstream and between hydrologically connected wetlands (Soons 2006). Animals in search of water may provide a much more targeted (or "directed") means of dispersal among all wetland types, which is essential to maintain the viability of wetland plant populations (Purves and Dushoff 2005; Kleyheeg 2015).

Both mammals and birds are able to transport large numbers of plant diaspores over long distances, but large migratory mammals have been subjected to massive prehistorical extinctions (Janzen 1984), and nowadays are restricted by movement barriers such as fences and inhabited areas, which birds can easily surpass. Given the abundance of waterbirds, their role in the directed dispersal of diaspores among wetlands is critical.

Although aquatic plants disperse via asexual propagules such as rhizomes or stem fragments, these propagules are typically more important for dispersal within a catchment by hydrochory (Santamaria 2002), or for short-distance dispersal by external transport. Dispersal among catchments is predominantly by internal or external transport of seeds. Although small floating plants such as *Lemna* or *Azolla* may be exceptions (fig. 6.1), they have limited resistance to desiccation during external transport (Coughlan et al. 2015).

Despite major advances in taxonomy and the discovery of cryptic species using molecular methods, Darwin's (1859) observation that aquatic plants have particularly broad distributions has stood the test of time. Aquatic plants have lower levels of endemism, and are more likely than terrestrial plants to occur on more than one continent. Within a genus such as *Ranunculus*, which has many European species, aquatic species have a greater latitudinal range and overall area of occupancy than do terrestrial species (Santamaria 2002). The biogeography of aquatic plants thus shows a lasting footprint of long-distance dispersal. Corresponding to their high dispersal ability, natural selection has honed aquatic plants with general purpose genotypes, high stress tolerance and high clonal persistence, all of which allows them to occupy large ranges.

The importance of seed dispersal for aquatic plants varies with the spatial configuration of wetlands in the landscape across fragmentation gradients which include latitudinal and climatic gradients. In Europe, the proportion of temporary aquatic habitats increases from north to south—and with it, the relative importance of sexual reproduction. In northern habitats, plants are more able to spread within a habitat and to persist from year to year in the absence of seed production (often overwintering as rhizomes). The chances of seedling establishment can be extremely low, owing to intense competition with established plants (Santamaria 2002). Hence, seeds of aquatic plants appear adapted for long-distance dispersal to unoccupied habitats rather than local dispersal within an already occupied habitat. In contrast, in the Mediterranean region of southern Europe, aquatic habitats are highly dynamic and often temporary, and suitable microhabitats for a given plant species often change greatly from one season or year to the next. Ponds and lakes often dry out completely in summer or during drought cycles. Hence, diaspores with dormant capacity (seeds or spores) are important at a local scale for survival of drought and for colonization of areas that become suitable in a given year. Seed dispersal *within* a wetland complex becomes more important, and may be more likely to be followed by successful establishment than in northern permanent habitats. Birds are also typically major seed dispersal vectors within a wetland complex, often moving the seeds to sites they could not reach by hydrochory (Figuerola et al. 2003; Brochet et al. 2010a). These latitudinal patterns explain why widespread pondweed species, such as *Potamogeton pectinatus*, invest more in seed production in southern than in northern populations (Santamaria et al. 2005).

De Vlaming and Proctor (1968) emphasized that because most aquatic plants are monoecious, a single viable diaspore dispersed to a new habitat

may be sufficient to establish a new population. Similarly Cruden (1966) pointed out that most plants with a distribution suggesting long-distance dispersal by shorebirds are self-compatible. Proctor (1980) showed for the Characeae that only bisexual or parthenogenetic taxa are present on isolated oceanic islands. In contrast, dioecious taxa are restricted to continental land masses and islands within a maximum range of 200 to 300 km, such that repeated dispersal events allow establishment of both sexes.

What Happens to Diaspores in the Waterbird Gut?

For almost all plant species whose seeds are ingested by ducks, some seeds survive gut transit (Brochet et al. 2009). Exceptions appear due to large seed size, which makes gut passage unlikely. Aquatic seeds that seldom survive passage through the waterbird gut include the large, soft seeds of the water lilies *Nymphaea alba*, *Nuphar lutea*, and *Nymphoides peltata* (Smits et al. 1989; Soons et al. 2008), which are favored food items of ducks (Tréca 1981). However, the seeds of these species are adapted for external transport (Smits et al. 1989; Cook 1990). They may also be secondarily dispersed by internal transport when they are in fish ingested by piscivorous birds. Such large seeds may also be regurgitated by waterbirds occasionally without damage (Kleyheeg 2015). During experiments, mallards sometimes regurgitate charophytes before they enter the gizzard (Malone 1966).

In an experimental study in which seeds of 23 wetland plant species were fed to mallards, the proportion of seeds retrieved from feces varied from 0 to 54%, with a negative relationship between seed volume and retrieval (Soons et al. 2008). In the same study, smaller seeds were retained for less time in the gut. In a similar study in which diaspores of eight species were fed to green-winged teal (*Anas crecca*), retrieval varied from 2 to 83% (Brochet et al. 2010b). Wongsriphuek et al. (2008) found that seed retrieval increased with higher fiber content among 10 wetland species fed to mallards. Retrieval was not related to seed size. Van Leeuwen et al. (2012) found in a meta-analysis that larger propagules, including plant seeds, have lower survival during passage through the waterfowl gut; but García-Álvarez et al. (2015) showed that there are exceptions with large, durable seeds, such as the invasive primrose *Ludwigia grandiflora* (Onagraceae).

The fact that many seeds survive gut processing by waterbirds can be explained by optimality modeling (Sibly 1981; van Leeuwen et al. 2012). Even when ducks are consuming a single preferred seed species which provides

a high assimilation rate, the diminishing returns from the digestion of the last fractions of seeds renders total digestion suboptimal. Since ducks are highly omnivorous, they may often consume and process a combination of different seed types with other plant or animal food, and retention time may be determined largely by the optimal strategy for digesting foods other than seeds.

Thus, Sibly's (1981) model would predict that seeds mixed with higher-quality food, such as animal pellets, should be retained for shorter periods than those mixed with lower-quality food such as plant leaves, as was observed with digestive markers by Charalambidou et al. (2005). Similarly, when food items are more available in the feeding environment and handling times are reduced, optimality theory predicts that gut passage rate can be increased, thus increasing the rate of diaspore survival. This expectation is supported by field studies, indicating that seed survival increases when ducks ingest seeds at a higher rate (Figuerola et al. 2002; Green et al. 2002).

Waterbirds are likely to select seeds partly on their nutritional quality, which is likely to be positively related to their digestibility and negatively related to their capacity to survive digestion. Thus, the breeding white-faced whistling duck (*Dendrocygna viduata*) and red-billed teal (*Anas erythrorhyncha*) fed largely on *Panicum schinzii* seeds, which had a particularly high fat content (Petrie 1996; Petrie and Rogers 1996). Given their bill morphology, it is difficult for ducks to reject relatively poor quality seeds mixed with other foods (Gurd 2006), and they typically ingest many kinds of seeds simultaneously (Brochet et al. 2012a). The digestive assimilation efficiency of seeds varies among bird species and even between sexes of a given waterbird species (Santiago-Quesada et al. 2009).

Variation in overall retention time between food items such as diaspores is partly related to variation in the time they are retained in the gizzard. Larger items tend to be retained longer, which explains why smaller seeds generally have shorter overall retention times (Soons et al. 2008; Kleyheeg 2015; but see Figuerola et al. 2010). Unlike frugivores, retention time in waterfowl is negatively related to body size, making smaller species better vectors (García-Álvarez et al. 2015).

The chance that a diaspore survives retention in the gizzard is related to the strength of the gizzard and to the amount of grit (small stones) present to crush food (Kleyheeg 2015). The size and quantity of grit varies between individuals and species of waterfowl in a manner related to diet, with herbivorous species having more grit (Figuerola et al. 2005a). Some

authors have suggested that shorebirds sometimes ingest hard seeds for the same reason they ingest grit: to help crush other food in the gizzard, rather than for direct nutritional benefit (Green et al. 2002). It is difficult to mimic natural conditions in captivity, and existing studies of seed survival and retention times may be misleading. Wild ducks tend to have larger gizzards and intestines than do captive ones (Charalambidou and Santamaría 2002), such that captive studies may tend to overestimate seed survival while perhaps underestimating retention times. On the other hand, the low activity levels of captive birds compared to those of wild ones, which spend much time swimming or flying, may lead to a major underestimation of the proportion of seeds that survive gut passage, as well as a slight overestimation of retention times (Kleyheeg et al. 2015).

Recent studies addressed the effects of passage through the waterbird gut on germinability (the probability of germination) and germination rate (the time taken to germinate) of seeds. As with terrestrial birds (Traveset 1998), the effects of gut processing by waterfowl vary. In some cases, gut processing increased germinability, but in other cases passage decreased it (Soons et al. 2008; Brochet et al. 2010b; García-Álvarez et al. 2015). The rate of germination is usually, but not always, increased by gut passage (Brochet et al. 2010b; Figuerola et al. 2010; García-Álvarez et al. 2015). The differences between studies are likely related to plant species–specific effects of gut passage on germination capacity.

Which Plants Are Dispersed by Ducks?

Given the shortage of studies that quantify viable diaspores moved by waterbirds in the field, and given that the great majority of diaspore types have some capacity to survive gut passage, diet studies that identify diaspores are of great interest. Many such studies exist for dabbling ducks, and reanalysis of these datasets sheds light on the variation in dispersal processes over space and time, as well as between specific plant and bird species. The frequency of a given seed type in the upper guts of ducks is a strong predictor of its frequency as a viable seed in faeces (Brochet et al. 2009).

We reviewed 70 studies of the diet of dabbling ducks in Europe and found that seeds of at least 445 plant species of 189 genera and 57 families were reported (table 6.1 and supplemental table S6.1 at www.press .uchicago.edu /sites/whybirdsmatter/). The species encompass a wide range of families, from Poaceae (grasses), with no obvious adaptations for

any means of dispersal, to Asteraceae (Compositae), with often complex adaptations for wind dispersal (such as the plume of dandelion seeds).

To find general patterns in the plant species dispersed by dabbling ducks, we analyzed 413 of the 444 plant species in Europe, for which quantitative data exist. We analyzed plant traits reflecting species' habitats, seed production, size, and dispersal capacity by wind and water. Species habitat can be estimated using Ellenberg indicator values (Ellenberg et al. 1991), which represent the optimum conditions at which European species occur along an environmental gradient. We looked at species occurrence along the following gradients: nutrient-poor to nutrient-rich (indicated by Ellenberg N values), dry to wet (Ellenberg F), and shaded to well-lit (Ellenberg L). Ellenberg values were taken from the PLANTATT database (Hill et al. 2004; extracted 5 December 2006). Species trait data used were seed production (measured as the number of seeds per individual plant, ramet, or tussock), seed size (measured as seed volume, in mm³), wind dispersal capacity as approximated by seed terminal velocity (measured as the constant falling rate of a seed in still air, after an initial short phase of acceleration, in ms⁻¹) and water dispersal capacity as approximated by seed buoyancy (measured as the percentage of seeds still floating after one week in water). Trait data were taken from the LEDA databse (Kleyer et al. 2008; extracted 13 July 2010).

Frequency distributions of the Ellenberg values of the species ingested by ducks were compared to those of all plant species for which Ellenberg data are available (fig. 6.3), showing that ducks feed disproportionally on plant species from sites of rich (but not extremely rich) fertility (Ellenberg N values 6–8), wet to inundated sites (Ellenberg F values 8–12), and habitats on the transition from semishaded to well-lit (Ellenberg L value 7). This analysis shows how plant species from wet, relatively nutrient-rich, and relatively open (but not too open) habitats have a greater probability of being dispersed by dabbling ducks.

On the other hand, in terms of numbers of species, fig. 6.3 indicates that most plant species that are present in duck diets, and which therefore are thought to be dispersed by ducks, are not aquatic but rather terrestrial, especially plants of moist soils (Hagy and Kaminski 2012). Small seeds in terrestrial plants are characteristic of early successional, light-rich environments. Whenever these seeds are washed or blown into wetlands, as during storms, they may be ingested and then dispersed by waterbirds. Wetlands are unsuitable habitat for many plant species whose seeds are taken there by rainfall (Gordon and van der Valk 2003). They may then

TABLE 6.1 **Seeds (oogonia for algae) found in digestive tracts of eight dabbling duck species in Europe (gadwall, garganey, mallard, marbled teal, pintail, shoveler, common teal, and wigeon). Taxonomy is after *Flora Europaea* (provided online by the Royal Botanic Garden of Edinburgh, accessed in 2013) for plants eaten. Most of the data for the mallard, pintail, and common teal come from the supporting information table provided online for the paper by Brochet et al. (2012a), supplemented by additional references. See table 6.1 extended online for more details (www.press .uchicago.edu/sites/whybirdsmatter/).**

ALGAE
Characeae
    Chara canescens
    Chara sp.
VASCULAR PLANTS
Alismataceae
    Alisma plantago-aquatica
    Baldellia ranunculoides
    Sagittaria sagittifolia
Amaranthaceae
    Amaranthus albus
    Amaranthus deflexus
    Amaranthus hybridus
    Amaranthus retroflexus
Araceae
    Calla palustris
Betulaceae
    Alnus glutinosa
    Alnus incana
    Betula pendula
    Betula pubescens
Boraginaceae
    Myosotis arvensis
    Myosotis scorpioides
Callitrichaceae
    Callitriche sp.
Caprifoliaceae
    Sambucus nigra
    Sambucus racemosa
    Viburnum lantana
Caryophyllaceae
    Arenaria sp.
    Cerastium sp.
    Lychnis flos-cuculi
    Spergula arvensis
    Spergularia marina
    Spergularia media
    Stellaria holostea
    Stellaria media
Ceratophyllaceae
    Ceratophyllum demersum
Chenopodiaceae
    Arthrocnemum fruticosum
    Arthrocnemum macrostachyum
    Atriplex hastata

TABLE 6.1 (*continued*)

Atriplex hortensis
Atriplex littoralis
Atriplex patula
Atriplex prostrata
Bassia hirsuta
Beta vulgaris
Chenopodium album
Chenopodium ficifolium
Chenopodium glaucum
Chenopodium murale
Chenopodium polyspermum
Chenopodium rubrum
Chenopodium vulvaria
Halimione pedunculata
Halimione portulacoides
Halocnemum strobilaceum
Salicornia europaea
Salsola soda
Suaeda maritima
Suaeda vera
Suaedea corniculata
Compositae
Artemisia sp.
Aster tripolium
Baccharis halimifolia
Bidens cernua
Bidens frondosa
Bidens tripartita
Chamomilla recutita
Cirsium arvense
Cirsium palustre
Cirsium vulgare
Filaginella uliginosa
Helianthus annuus
Hieracium umbellatum
Inula sp.
Senecio aquaticus
Silybum marianum
Soliva sp.
Convolvulaceae
Calystegia sepium
Convolvulus arvensis
Corylaceae
Carpinus betulus
Cruciferae
Brassica napus
Cochlearia sp.
Coronopus squamatus
Lepidium sp.
Nasturtium microphyllum
Nasturtium officinale

TABLE 6.1 (*continued*)

    Rapistrum sp.
    Rorippa amphibia
Cyperaceae
    Carex acuta
    Carex acutiformis
    Carex aquatilis
    Carex arenaria
    Carex bohemica
    Carex canescens
    Carex chordorrhiza
    Carex curta
    Carex disticha
    Carex divulsa
    Carex elata
    Carex elongata
    Carex extensa
    Carex flacca
    Carex flava
    Carex globularis
    Carex hirta
    Carex hispida
    Carex lasiocarpa
    Carex limosa
    Carex magellanica
    Carex nigra
    Carex otrubae
    Carex ovalis
    Carex pallescens
    Carex panicea
    Carex paniculata
    Carex pilulifera
    Carex pseudocyperus
    Carex riparia
    Carex rostrata
    Carex tomentosa
    Carex trinervis
    Carex vesicaria
    Carex vulpina
    Carex sp.
    Cladium mariscus
    Cyperus difformis
    Cyperus michelianus
    Cyperus serotinus
    Eleocharis acicularis
    Eleocharis multicaulis
    Eleocharis ovata
    Eleocharis palustris
    Eleocharis uniglumis
    Eriophorum vaginatum
    Fimbristylis sp.
    Schoenus nigricans
    Scirpus lacustris

TABLE 6.1 (*continued*)

 Scirpus litoralis
 Scirpus maritimus
 Scirpus mucronatus
 Scirpus setaceus
 Scirpus sylvaticus
 Scirpus triqueter
Elaeagnaceae
 Elaeagnus angustifolia
Elatinaceae
 Elatine hydropiper
Empetraceae
 Empetrum nigrum
Equisetaceae
 Equisetum fluviatile
Ericaceae
 Calluna vulgaris
 Vaccinium myrtillus
 Vaccinium uliginosum
 Vaccinium vitis-idaea
Fagaceae
 Quercus faginea
 Quercus robur
Geraniaceae
 Geranium dissectum
 Geranium robertianum
Guttiferae
 Hypericum hirsutum
Haloragaceae
 Myriophyllum spicatum
 Myriophyllum verticillatum
Hippuridaceae
 Hippuris vulgaris
Hydrocharitaceae
 Hydrocharis morsus-ranae
 Vallisneria spiralis
Iridaceae
 Iris pseudacorus
Juncaceae
 Cyperus serotinus
 Juncus acutiflorus
 Juncus articulatus
 Juncus compressus
 Juncus effusus
 Juncus filiformis
 Juncus gerardi
 Juncus inflexus
 Juncus littoralis
 Luzula spicata
Juncaginaceae
 Triglochin maritima

TABLE 6.1 (*continued*)

Labiatae
    Ajuga reptans
    Galeopsis speciosa
    Galeopsis tetrahit
    Lycopus europaeus
    Mentha aquatica
    Prunella vulgaris
    Scutellaria galericulata
    Stachys palustris
Leguminosae
    Astragalus sp.
    Lotus corniculatus
    Lotus uliginosus
    Medicago arabica
    Medicago lupulina
    Medicago sativa
    Pisum sp.
    Trifolium campestre
    Trifolium dubium
    Trifolium fragiferum
    Trifolium pratense
    Trifolium repens
    Trifolium squamosum
    Vicia cracca
Lemnaceae
    Lemna gibba
Lythraceae
    Lythrum salicaria
Malvaceae
    Althaea officinalis
    Malva sp.
Marsileaceae
    Pilularia sp.
Menyanthaceae
    Menyanthes trifoliata
Najadaceae
    Najas gracillima
    Najas indica
    Najas marina
    Najas minor
Nymphaeaceae
    Nuphar lutea
    Nymphaea alba
    Nymphoides peltata
Onagraceae
    Epilobium hirsutum
    Ludwigia peploides
Oxalidaceae
    Oxalis sp.
Papaveraceae
    Chelidonium majus
    Papaver sp.

TABLE 6.1 (*continued*)

Parnassiaceae
    Parnassia palustris
Plantaginaceae
    Plantago lanceolata
    Plantago major
    Plantago maritima
    Plantago media
Plumbaginaceae
    Armeria maritima
    Limonium vulgare
Poaceae
    Agrostis stolonifera
    Alopecurus geniculatus
    Alopecurus myosuroides
    Alopecurus pratensis
    Anthoxanthum odoratum
    Apera spica
    Arrhenatherum sp.
    Avena fatua
    Avena sativa
    Bromus secalinus
    Bromus sterilis
    Cynodon dactylon
    Digitaria sanguinalis
    Echinochloa crus-galli
    Eleusine indica
    Elymus pungens
    Elymus repens
    Eragrostis sp.
    Festuca arundinacea
    Festuca rubra
    Glyceria declinata
    Glyceria fluitans
    Glyceria maxima
    Glyceria plicata
    Holcus lanatus
    Hordeum distichon
    Hordeum hystrix
    Hordeum marinum
    Hordeum secalinum
    Hordeum vulgare
    Leersia oryzoides
    Lolium multiflorum
    Lolium perenne
    Milium sp.
    Oryza sativa
    Panicum miliaceum
    Parapholis strigosa
    Paspalum oaginatum
    Paspalum paspalodes
    Paspalum vaginatum

TABLE 6.1 (*continued*)

    Phalaris arundinacea
    Phleum pratense
    Phragmites australis
    Poa annua
    Poa bulbosa
    Poa pratensis
    Poa trivialis
    Polypogon sp.
    Puccinellia distans
    Puccinellia fasciculata
    Puccinellia maritima
    Secale cereale
    Setaria italica
    Setaria pumila
    Setaria verticillata
    Setaria viridis
    Sorghum bicolor
    Spartina townsendii
    Triticum aestivum
    Triticum sp.
    Zea mays
Polygonaceae
    Fagopyrum esculentum
    Fallopia convolvulus
    Polygonum amphibium
    Polygonum aviculare
    Polygonum hydropiper
    Polygonum lapathifolium
    Polygonum minus
    Polygonum mite
    Polygonum persicaria
    Polygonum viviparum
    Rumex acetosa
    Rumex acetosella
    Rumex aquaticus
    Rumex conglomeratus
    Rumex crispus
    Rumex hydrolapathum
    Rumex maritimus
    Rumex obtusifolius
    Rumex palustris
    Rumex pulcher
Pontederiaceae
    Heteranthera limosa
    Heteranthera reniformis
Potamogetonaceae
    Potamogeton acutifolius
    Potamogeton berchtoldii
    Potamogeton gramineus
    Potamogeton lucens
    Potamogeton natans
    Potamogeton nodosus

TABLE 6.1 (*continued*)

Potamogeton obtusifolius
Potamogeton pectinatus
Potamogeton perfoliatus
Potamogeton polygonifolius
Potamogeton pusillus
Potamogeton trichoides
Primulaceae
Glaux maritima
Lysimachia vulgaris
Ranunculaceae
Ranunculus acris
Ranunculus baudotii
Ranunculus bulbosus
Ranunculus flammula
Ranunculus hederaceus
Ranunculus lingua
Ranunculus repens
Ranunculus sardous
Ranunculus sceleratus
Ranunculus trichophyllus
Thalictrum sp.
Resedaceae
Reseda lutea
Reseda luteola
Rosaceae
Cotoneaster sp.
Crataegus laevigata
Crataegus monogyna
Filipendula ulmaria
Fragaria vesca
Potentilla anserina
Potentilla palustris
Prunus cerasus
Prunus spinosa
Pyrus malus
Rosa canina
Rosa multiflora
Rubus arcticus
Rubus chamaemorus
Rubus fruticosus
Rubus sp.
Sorbus aucuparia
Rubiaceae
Galium aparine
Galium palustre
Galium tricornutum
Ruppiaceae
Ruppia cirrhosa
Ruppia maritima
Salicaceae
Salix sp.

TABLE 6.1 (*continued*)

Scheuchzeriaceae
    Scheuchzeria palustris
Scrophulariaceae
    Linaria arvensis
    Linaria vulgaris
    Odontites verna
    Rhinanthus minor
    Scrophularia auriculata
    Scrophularia nodosa
    Verbascum sp.
    Veronica anagallis-aquatica
    Veronica beccabunga
    Veronica catenata
    Veronica hederifolia
    Veronica persica
Solanaceae
    Solanum dulcamara
    Solanum lycopersicum
    Solanum nigrum
    Solanum tuberosum
Sparganiaceae
    Sparganium angustifolium
    Sparganium emersum
    Sparganium erectum
    Sparganium minimum
Typhaceae
    Typha latifolia
Umbelliferae
    Anthriscus sylvestris
    Cicuta virosa
    Falcaria vulgaris
    Oenanthe aquatica
    Oenanthe fistulosa
    Torilis japonica
Urticaceae
    Urtica dioica
Valerianaceae
    Valerianella sp.
Vitaceae
    Vitis vinifera
Zannichelliaceae
    Zannichellia palustris
Zosteraceae
    Zostera angustifolia
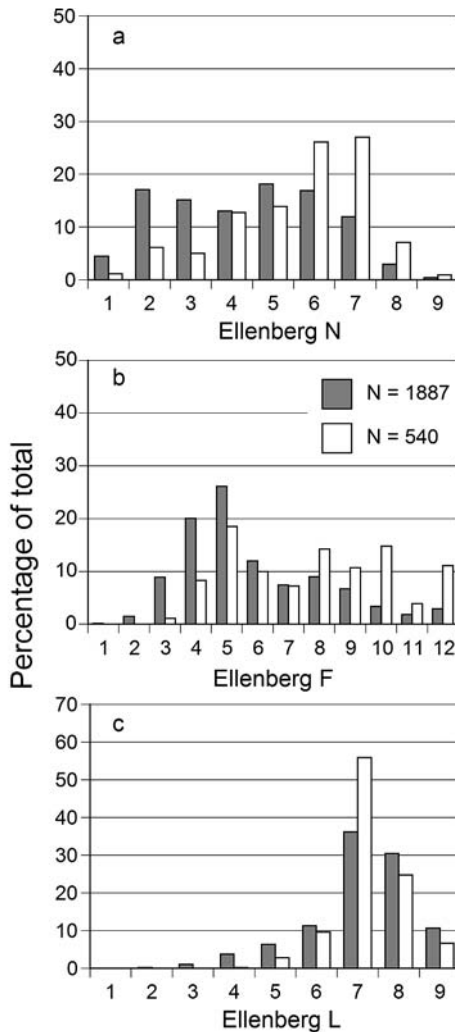   *Zostera marina*
    Zostera noltii

FIGURE 6.3. Analysis of plant species identified from the gut content of *Anas* dabbling ducks in Europe, in comparison to all European plant species for which Ellenberg values are available, showing that ducks feed disproportionately on plant species at (a) sites of rich fertility (Ellenberg *N* values 6–8), at (b) wet to inundated (open water) sites (Ellenberg *F* values 8–12), and at (c) habitats in transition from being semishaded to well lit (Ellenberg *L* value 7). The gray bars indicate the distribution of Ellenberg values over all plant species; the white bars indicate the distribution for species from duck gut contents. The total number of data points corresponding to dark and light bars for each graph are indicated in the middle panel.

be returned to terrestrial habitats by waterbirds—for example, by def-
ecation on the shoreline or during flight, or when moved to temporary
ponds or flooded grasslands that later dry out.

Analysis of the plant species identified from the gut contents of dabbling
ducks in comparison to all plant species for which trait data are available
in the LEDA database (fig. 6.4), shows that the ducks feed more or less
proportionately on species relative to their seed production and seed buoy-
ancy, but disproportionately more on plant species with seeds of relatively
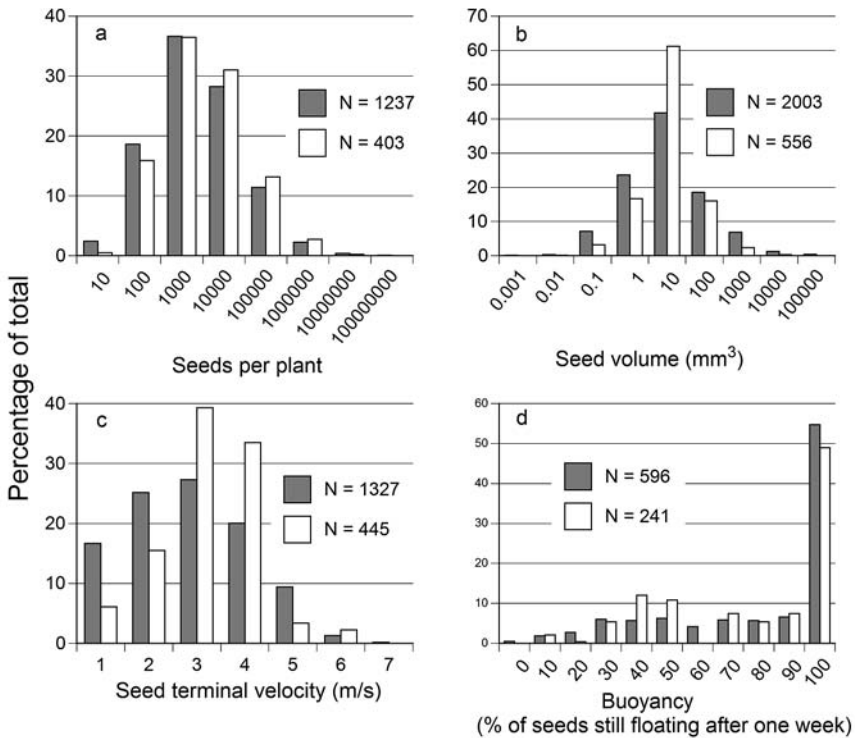

FIGURE 6.4. Analysis of the plant species identified from the gut content of *Anas* dabbling
ducks in Europe, in comparison to all European plant species for which dispersal-related trait
data are available, showing that the ducks feed more or less proportionately on species rela-
tive to their seed production (a) and seed buoyancy (d), but disproportionately on plant spe-
cies with seeds of relatively small sizes (b: 1–10 mm^3) and high terminal velocities (c: 2–4 m/s).
The gray bars indicate the distribution of trait values over all plant species; the white bars
indicate the distribution for species from duck gut contents. The total number of data points
included in the histograms is indicated in each panel.

small sizes (1–10 mm^3) and high terminal velocities (2–4 ms^{-1}). Thus, plant species with relatively small seeds, lacking specific adaptations for wind dispersal, have a greater probability of being dispersed by dabbling ducks.

From this analysis it becomes clear that *Anas* ducks feed on and potentially disperse a very wide range of plant species, and that their role in plant dispersal is very important not only for aquatic species but for moist-soil and terrestrial species within the hydrological catchments of wetlands. This includes many species that on the basis of seed morphology would not be classified by plant ecologists as being primarily dispersed by animals. Such generalizations from measured traits will therefore underestimate a species' potential for dispersal by waterfowl.

Rarefaction analyses (fig. 6.5) show that, in a given study site, ducks are dispersing a high diversity of plant species, and even studies of several hundred duck individuals do not reach an asymptote in taxonomic richness of seeds. How many vascular plant species are being dispersed by ducks in Europe is anybody's guess, and while our review of the literature of dabbling duck diet has identified 445 taxa, the considerable differences between the few localities where detailed studies have been conducted suggests that, on a continental scale, thousands of plant species are being dispersed.
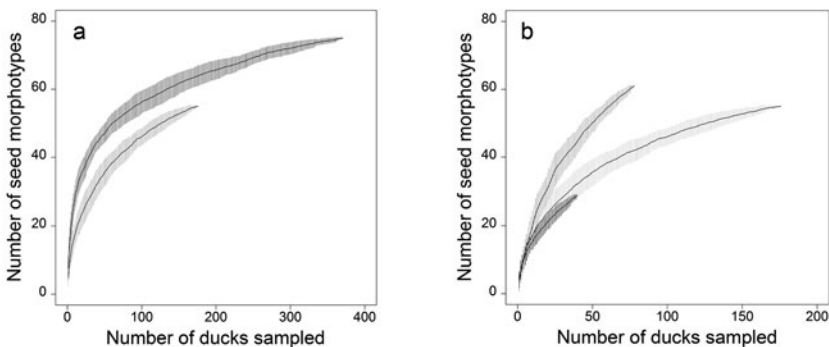

FIGURE 6.5. Rarefaction curves comparing the diversity of seed morphotypes found in the esophagus or gizzard of mallards and green-winged teals, showing means ± s.e. from random permutations of 50 birds: (a) mallard (light) and green-winged teal (dark), from the Camargue in France; (b) mallard from the Camargue (light), a study in the Netherlands (dark), and the Ebro Delta in Spain (black). Note the change in scale on the *X* axis. Data reanalyzed from Brochet et al. 2012a (Camargue), Brochet et al. unpublished (Ebro), and Kleyheeg et al. unpublished (Netherlands). Adjustments were made to the Netherlands data set to ensure comparability (e.g., merging *Carex* species as in the Camargue study).

Can Diaspore Morphology Be Used to Predict Which Diaspores Are Dispersed by Waterbirds?

Much general literature on plant dispersal has been based on the assumption that diaspore morphology provides reliable information as to dispersal means (an idea developed at length by van der Pijl 1972). However, waterbirds throw a spanner in the works of such a concept, as there is no way to reliably predict on the basis of morphology—other than (to some extent) size—which diaspores they will disperse, and the list of plant species potentially dispersed by waterbirds would seem to be enormous (perhaps all non-forest species with diaspores with a volume of less than ca. 10 mm3 which lie in hydrological catchments frequented by waterbirds). On the basis of small size and lack of fleshy fruits, Tiffney (2004) suggested that Cretaceous angiosperms were predominantly dispersed by abiotic means. Yet waterbird communities, especially shorebirds, were well established by the end of the Early Cretaceous (Lockley et al. 1992; Kim et al. 2012), and they were likely to be important diaspore vectors from the very beginning. Tiffney points out that the diaspores of most Cenozoic herbs do not exhibit clear morphological adaptations to vertebrate dispersal (i.e., they lack flesh). However, this cannot be taken as evidence against dispersal by waterbirds. Tiffney argues that biotic dispersal became more widespread and important in the Tertiary than in previous periods, but again by using flesh as the indicator of such dispersal. Likewise, we question Tiffney's assumption that a reduction in diaspore size during climate cooling (during the Tertiary) or with increasing latitude (in modern diaspores) can be taken to indicate a reduced role for biotic dispersal. Janzen (1984) effectively makes the same point by listing many plant genera, classically assumed to disperse by wind or water, which are regularly dispersed by large mammals.

Carlquist (1967) recognized the importance of shorebirds and other waterbirds in the dispersal of plants to oceanic islands, and argued that seed morphology could be used to separate seeds dispersed internally from those dispersed externally. Carlquist and Pauly (1985) later provided experimental support for a link between seed morphology and adhesive capacity for external transport. Nevertheless, many of the plants predicted by Carlquist (1967) to disperse externally are now known to be readily dispersed internally.

On the basis of a diet review and the intensive study of diaspore dispersal by green-winged teals, Brochet et al. (2009, 2010a) found that seed

species dispersed by external transport could not be identified by presence of hooks, barbs, or other structures that might readily be interpreted as adaptations for external attachment. Indeed, there was no clear difference in morphology between seeds found on the outside and the inside of green-winged teals, with much overlap between dispersal modes. In summary, it seems that there are no reliable morphological means, other than seed size, to predict which seed types are dispersed by waterbirds, whether internally or externally. Likewise, the extensive literature on plant dispersal modes that makes predictions based on seed morphology (e.g. Tiffney 2004; Thorsen et al. 2009) seems unreliable in that it overlooks dispersal by waterbirds of seeds that lack the classical predictors of zoochory.

When Are Diaspores Dispersed by Waterbirds and in What Direction?

Internal transport of diaspores by waterbirds occurs throughout the annual cycle, even though diaspore production itself is often limited seasonally (Kleyheeg 2015). Ducks and other waterbirds frequently ingest diaspores from the seed bank in wetland sediments, where their availability can remain high even at the end of winter (Green et al. 2002). Although migratory ducks in the Northern Hemisphere typically consume more diaspores and fewer invertebrates in winter, they still ingest a variety of diaspores during the breeding season (Green et al. 2002; Rodríguez-Pérez and Green 2006). Few studies examine diets of ducks living in other climatic regions, and some found that seeds dominate the adult diet during the breeding season (Petrie 1996; Petrie and Rogers 1996). Outside the breeding season, and especially in winter, ducks and many other waterbirds typically undertake regular local movements between sites used for feeding and for resting, and these are often independent waterbodies (Kleyheeg 2015). Since most preening is carried out at the resting sites, diaspores can be carried on feathers or feet to these latter sites before being removed by preening. Thus, there is likely to be directional dispersal from feeding to resting sites both by endo- and epizoochory (Kleyheeg 2015). Studies of duck diet on stopover sites during spring and autumn migration in North America confirm that seeds are ingested in abundance on migration by dabbling and diving ducks, and that, while seeds of some plant species are recorded in the diet in greater abundance in autumn, others are found more in spring (Green et al. 2002).

Figuerola et al. (2002, 2003) conducted a particularly detailed field study of internal transport in Doñana, Spain, Europe's most important wintering site for waterfowl (Rendon et al. 2008). When comparing early winter (November and December, when wintering ducks are still arriving) with late winter (late February, when birds are leaving), they found no consistent difference in rates of seed dispersal, but instead a statistical interaction between season and bird species. For example, numbers of *Ruppia maritima* seeds were higher in late winter in mallard and northern pintail (*Anas acuta*) feces, and were lower in late winter for Eurasian coot, but did not change for northern shoveler (*A. clypeata*). Numbers of *Salicornia* seeds were higher in early winter for pintail, mallard, and coot, but there was no seasonal difference for shoveler.

Brochet et al. (2010a) found no seasonal variation between early and late winter in the overall rates of diaspore dispersal by green-winged teals in the Camargue when considering intact diaspores found at the end of the lower gut. However, the relative composition of different plant taxa in the diet of green-winged teals did vary during the course of the winter (Brochet et al. 2012a). Diaspores of some species (e.g., *Chara* spp.) were more frequently ingested (and hence dispersed) in early winter, while others (e.g., *Echinochloa* sp.) were more frequent in late winter. Likewise, the diet composition of mallards in the Netherlands varied greatly over the course of autumn and winter (Kleyheeg 2015).

In conclusion, seasonality influences both the distance and direction of plant dispersal by migratory waterbirds. Plant dispersal occurs year-round, and rates of dispersal may vary among sites and bird species in a manner specific to each plant species. Spring migration is likely to be particularly important for the dispersal of plants responding to climate change, and there is strong potential for long-distance dispersal by waterbirds during this period, even for plants that produce diaspores in summer or autumn.

Specificity or Redundancy: Potential Coevolution between Waterbirds and Diaspores

Although duck species can differ significantly in the number of diaspores carried for a given plant species, European studies show that, in a given wetland at a given time, different dabbling ducks overlap greatly in the plant species they consume and disperse (fig. 6.6; see also Figuerola et al.

2003). Although some duck species appear consistently more important as vectors (e.g., green-winged teal and mallard being more important than northern pintail in fig. 6.6), this is largely determined by the relative abundance of the duck species at that site. Green-winged teal and northern shoveler seem consistently to disperse a greater variety of seeds than do mallard on an individual basis (Brochet et al. 2009; see also fig. 6.5a), but the sheer abundance of mallard in some wetlands can make them the dominant vector for any plant species (e.g., in the Ebro delta; fig. 6.6). In Australia, Raulings et al. (2011) also found high similarity in the plant species dispersed by three duck species by both endo- and epizoochory.

Diaspore size influences the relative importance of different waterfowl species as vectors. Ducks with finer lamellae in their bills (such as the northern shoveler or the green-winged teal) tend to ingest relatively smaller diaspores than do ducks with coarse lamellae (such as mallard; Brochet et al. 2012b). We reanalyzed data from Brochet et al. 2012a for teal and mallard, taking the 11 diaspore types that were recorded in at least 20% of individuals of at least one of the duck species. The difference in the mean number of diaspores per bird (in the esophagus or gizzard) between mallard and teal was significantly correlated with diaspore mass, both in early and late winter (Spearman's correlation coefficient $rs = 0.57$, 0.56 respectively; $P < 0.001$). This pattern largely explains the differences between mallard and teal for individual plant species. For example, *Potamogeton pectinatus* and *P. nodosus* seeds are much larger than *P. pusillus* seeds, and mallards are particularly important vectors for the first two. Ducks with finer lamellae also tend to disperse a larger number of plant taxa (fig 6.5a and Figuerola et al. 2003).

The high degree of overlap among plant species dispersed by different duck species is also found across different waterbird families, as is shown by comparison of the plants recorded in diets of gulls by Calvino-Cancela (2011) with those recorded in ducks by Brochet et al. (2009). Likewise, the diaspores found in the guts of Eurasian coot and gadwall in the Camargue were very similar (Allouche and Tamisier 1984). Furthermore, seeds dispersed by terrestrial and aquatic bird species overlap. For example, viable *Sonchus oleraceus* seeds are dispersed both by shorebirds (Sánchez et al. 2006) and by Eurasian bullfinch *Pyrrhula vulgaris* (W. E. Collinge in Ridley 1930). Five (*Plantago lanceolata*, *Ranunculus repens*, *Rumex crispus*, *Polygonum aviculare*, *Galium aparine*) of 17 species recorded to have germinated from songbird droppings by Collinge (in Ridley 1930) were listed in duck diet in Europe by Brochet et al. (2009). Similarly, Heleno et al.
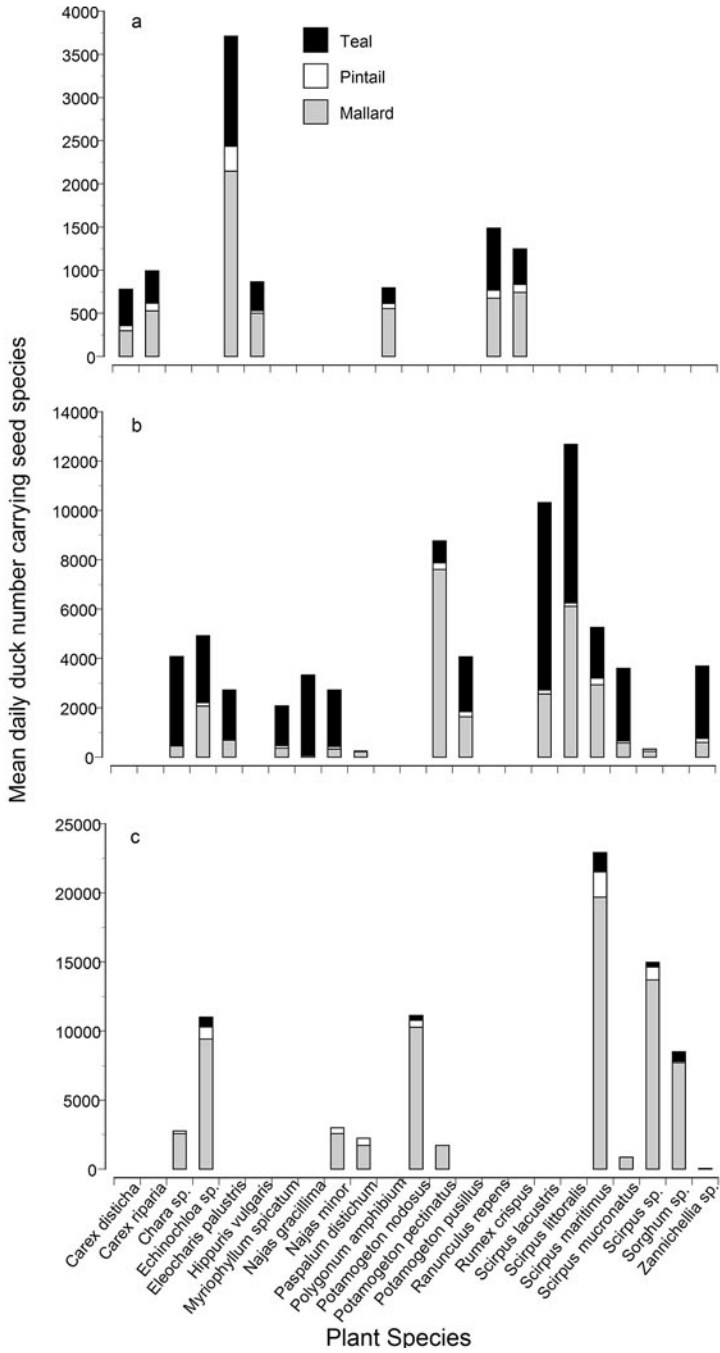
(2011) found that passerines dispersed Juncaceae, Cyperaceae and many other seeds without fleshy fruits.

Janzen (1984) envisaged that, prior to human intervention, large migratory mammals such as bovids, proboscideans, glyptodonts, or antilocaprids would have been the most important vectors of diaspores of many aquatic herbs of shallow seasonal marshes, which are now dependent on waterfowl. It is startling how many plant genera associated with pastures are dispersed by large mammals (Janzen 1984), and are also frequently dispersed by waterfowl (e.g. *Plantago*, *Medicago*, *Chenopodium*, *Carex*, *Juncus*, *Ranunculus*, *Polygonum*, *Atriplex*, *Paspalum*). Janzen speculated that waterfowl "probably offer only a pale shadow of what once could have been massive seed flow by large herbivores." If he is right, that only increases the importance of the role of waterbirds in conservation of modern ecosystems. Sumoski and Orth (2012) experimentally compared the potential of three fish species, a turtle, and the lesser scaup (*Aythya affinis*) to vector seeds of the seagrass *Zostera marina*. The duck was found to have a maximum seed dispersal distance at least 13 times greater than that of any other vector.

Diaspores dispersed by waterbirds are also dispersed by abiotic means, and both may select for diaspore characteristics simultaneously. Diplochory, in which the same individual seed is moved in successive steps, both by birds and by other processes, between the mother plant and germination site (Vander Wall 2004), may be common in waterbird-dispersed plant species. Van der Pijl (1972, 1982) recognized that diplochory as a combination of hydro- and endozoochory by waterbirds occurs frequently among Poaceae and Cyperaceae, and as a combination of zoochory and anemochory among Juncaceae and Cyperaceae. Seeds of dry habitats can be transported by waterbirds after being washed or blown into wetlands

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FIGURE 6.6. Spatial variation in the dispersal potential of different seeds by different dabbling ducks. The mean number of individuals of green-winged teal (black), mallard (gray), and northern pintail (white) carrying at least one seed of each seed type are presented, on the basis of extrapolating the gut contents by the winter counts for that species, and averaged for the whole winter period. Gut content data taken from (a) Thomas 1982, for the Ouse washes in England (1969–72, esophagus plus gizzard), (b) Pirot 1981, for the Camargue in France (1964–81, esophagus), and (c) Brochet et al. unpublished, for the Ebro delta in Spain (1992–95, oesophagus plus gizzard). Winter counts from the above years were obtained from the British Trust for Ornithology for the Ouse washes, from Tour du Valat for the Camargue, and from Martí and del Moral 2002 for the Ebro Delta. Only seed types present in at least 20% of individuals of one duck species in one study are included.

(Cruden 1966). The presence of seeds of so many nonaquatic plants in the diet of ducks supports this, as does our review of the buoyancy and terminal velocity of those seeds (fig. 6.4).

In summary, the coevolutionary interaction between most plant species and waterbird species is likely to be very "diffuse," with little evidence for potentially tight coadaptation between a given disperser and a given propagule. Waterbirds disperse many diaspore types that are also dispersed by mammals, terrestrial birds or other animals, and/or by wind or water. Moreover, except in landscapes of low species richness such as oceanic islands, a plant regularly dispersed by one waterbird species is likely to be dispersed by several others, with considerable redundancy between the roles of different vectors.

Are Any Diaspores Adapted for Internal Transport by Waterbirds?

Contrary to van der Pijl (1972) and his assumption that waterbirds dispersed "non-adapted diaspores," and despite the diffuse interactions among waterbirds and plants, the relationship between some plants (e.g., some Cyperaceae, pondweeds, and Characeae) and waterbirds seems close enough so that diaspores may be dependent on internal transport by waterbirds, with the possibility of adaptation to these vectors by natural selection. Ridley (1930) proposed that the fleshy red disc in which the stony black achenes of *Scleria sumatrensis* (Cyperaceae) are supported is an adaptation to visually attract birds, possibly rails. Other authors, such as De Vlaming and Proctor (1968) and Morton and Hogg (1989), suggested that small, dry, hard nutlike seeds are adaptations for dispersal by waterbirds. De Vlaming and Proctor (1968) suggested that there is a phylogenetic component to such adaptation, with Cyperaceae, for example, being more adapted than Poaceae and Compositae (Asteraceae).

Small diaspore size, often assumed to be an adaptation for abiotic dispersal, especially by wind (Tiffney 2004), also favors waterbird dispersal (fig. 6.4), and these vectors could potentially also exert selection pressure for small size. For example, Charophyte oospores are particularly small, and were the most abundant diaspore in the intestines of green-winged teals (Brochet et al. 2010a).

Janzen (1984) argued that many herbaceous plants evolved small, hard, numerous seeds with dormancy as adaptations for internal trans-

port by large mammals, even though these are amongst the "non-adapted diaspores" of van der Pijl (1972). Likewise, such diaspore features could favor, or even be selected for, internal transport by waterbirds (Kleyheeg 2015). As with seed dispersal by herbivorous mammals (Janzen 1984), larger seeds tend to have longer gut retention times in waterbirds, and therefore a greater chance of digestion and mortality. Investment in smaller seeds ensures both greater seed production and an increased probability of dispersal to a suitable microhabitat.

As suggested for seed dispersal by herbivorous mammals (Janzen 1984), selection for a seed coat that loses some resistance to germination cues during passage through the waterbird gut depends on whether the potential advantages for rapid germination following dispersal outweigh the potential advantages of delaying germination until some seasonal or successional cue appears in the habitat. In the case of aquatic diaspores, such a cue may include salinity, which itself can vary spatially, seasonally, and annually within a wetland complex. Espinar et al. (2004) found that the influence of gut passage on the germination of *Scirpus litoralis* seeds depends critically on salinity. Passage increased the germination rate at low salinities, but decreased it at high salinities. This response by the plant is potentially adaptive. When subjected to a similar experiment, seeds of *Juncus subulatus* survived gut passage, but exhibited no similar response to salinity variation (Espinar et al. 2006).

The proportion of diaspores destroyed during waterbird gut passage varies greatly (Soons et al. 2008; Brochet et al. 2010b). Nevertheless, even diaspore mortalities of more than 50% during gut passage are not good evidence that those diaspores are not adapted to dispersal by that vector (Janzen 1984). If waterbirds direct diaspores to microhabitats that are suitable for establishment, then high mortalities can be compensated for. Many terrestrial plants have toxic seeds to deter seed predators. The absence of toxic seeds among wetland plants supports the suggestion that these plants are partially adapted to passive dispersal by waterbirds. If, for example, Cyperaceae or pondweed seeds are not adapted for internal transport by waterbirds, then why aren't they toxic so as to avoid seed predation?

However, in the absence of pulp or other tissues that serve to attract animal vectors, it is very hard to establish what selective forces have led to the particular characteristics of diaspores of a given plant species. Not only are diaspores exposed to other modes of biotic and abiotic dispersal, their features are also selected to favor provision of adequate resources for the seedling, and/or survival in the soil or sediment seed bank.

Is Dispersal Effective? Do Seedlings Get Established after Dispersal?

Our knowledge about waterbird-mediated diaspore dispersal has rapidly increased in recent years, yet some aspects remain little studied. An essential question yet to be answered is: How effective is diaspore dispersal by waterbirds? Seed dispersal effectiveness can be expressed as "the number of new adult plants produced by the dispersal activities of a disperser" (Schupp 1993). This is the result of a series of events (or components of dispersal): ingestion of a certain number of seeds, digestion of a proportion thereof in the digestive tract, excretion in a certain habitat type, seed survival and germination, and plant survival until reproduction. Each of these events is hard to quantify under field conditions (see Herrera et al. 1994 for an example from a terrestrial system). To follow the whole cascade for individual seeds is essentially impossible. Although some separate components are now reasonably well studied for waterbird-plant systems, others are not. In particular, research on establishment success following seed dispersal is in its infancy, and has to date focused only on aquatic plants.

Aquatic habitats, compared to terrestrial habitats, provide ecological conditions that are relatively unsuitable for seed germination and seedling establishment (Santamaria 2002). In permanent habitats, clonal populations may persist for many years, even centuries, in the complete absence of seedling establishment. Asexual propagules, such as plant fragments, may disperse more successfully by hydrochory than seeds, owing to their higher establishment capacities. Their passage through the waterbird gut and subsequent dispersal must affect a seed's chances of success, but so far most research has focused simply on documenting the influence of gut passage on germination under laboratory conditions, and specifically on germination rate and germinability.

Competition in aquatic plant populations peaks during the growing season. Seeds might compensate for their poor competitive ability in comparison to established plants or vegetative propagules (which are produced only during the growing season) by their early arrival into a habitat via waterbirds and by early germination, which allows them to reach greater size before competition for light and other resources intensifies. Fennel pondweed (*P. pectinatus*) seeds grown in mesocosms (in the absence of competition or herbivory) were more likely to germinate early in winter

when they had passed through a duck gut, although this early start had no effect on the plants' size at the end of the growing season (Figuerola et al. 2005b). Wigeongrass (*Ruppia maritima*) seeds planted in a marsh frequented by a high density of wintering waterfowl were less likely to produce mature plants when they had passed through the guts of ducks, because earlier germination left them more exposed to herbivory (Figuerola and Green 2004). Gut passage has been shown to accelerate germination in various other plant species, although this effect can be masked by exposure of seeds to cold temperatures prior to experiments (Brochet et al. 2010b), and may generally be dependent on water salinity (Espinar et al. 2004). In short, much more research is needed on the consequences of seed dispersal by waterbirds and gut passage for the establishment success of plants.

Conclusions and Benefits to People

Waterbirds are major vectors for a wide variety of plants outside of closed forest habitats, both in wetland and in terrestrial habitats. Tens of thousands of plant species worldwide are likely to benefit from waterbird dispersal for colonization of new habitats, directed dispersal to suitable but hydrologically unconnected sites, gene flow, enhanced germination, and escape from areas of high mortality. Nevertheless, a lack of basic research currently makes it impossible to estimate how many plant species are dispersed by waterbirds and how many waterbird species are effective dispersers for each taxonomic group of plants. Indeed, the limits to which plants can be effectively dispersed by waterbirds are still unclear. Other animals are often alternative vectors for the same plant species, but migratory waterbirds are often highly abundant and are uniquely able to disperse over long distances. Given the recent extinctions and losses of large mammals connecting habitat patches, the role of waterbirds in the dispersal of plants across and between landscapes is likely to have increased—and to increase further in the future. Under the ongoing fragmentation of natural habitats, the ability of waterbirds to fly across barriers is critical. The distances that diaspores are moved by waterbirds remain unclear and little studied, but maxima of hundreds or thousands of kilometers are likely for many migratory species (Viana et al. 2013; Kleyheeg 2015).

Diaspore dispersal by waterbirds is an ecosystem service—specifically, a "supporting service," according to a common classification (MEA

2005)—that is vital for the maintenance of plant biodiversity and connectivity between populations. Anatidae and other waterbirds play an essential role in the colonization and regeneration of new and restored wetlands by aquatic flora and fauna. Waterbirds play a vital role in maintaining connectivity between aquatic communities in isolated aquatic systems, and thus in maintaining species and genetic diversity (Amezaga et al. 2002). In many cases, plants that are dependent on waterbirds for their dispersal are keystone species—notably pondweeds and other submerged plants. The benefits these plants provide to humans are largely indirect, through control of soil erosion and sedimentation, flood prevention, water purification, carbon sequestration, providing essential habitat for fish, and so on. However, all of these are essential to humans. Direct benefits can also be provided—for example, from the Juncaceae and Cyperaceae that are traditionally used by humans for thatching. There may also be costs, because waterbirds can often be effective at spreading alien plants, including weeds.

In the past, passive dispersal of wetland plants by birds probably enabled the quick recolonization of extensive areas following glacial retreat (Santamaria 2002). Now, and increasingly in the future, plants require waterbirds as vectors if they are to colonize areas that become suitable under climate change. Waterbirds are already shifting their distributions in response to climate change (Visser et al. 2009; Godet et al. 2011), though they may track the changes with time lags that potentially have negative consequences for their own population viability. There is already evidence that waterbirds are enabling the colonization of polar regions by new plant species (Klein et al. 2008). It remains to be seen which plants will be able to shift their distributions fast enough via birds to avoid a crash in population range and size. What seems certain is that many species would have much less chance of shifting ranges if it were not for waterbirds. The ecosystem services that waterbirds provide by dispersing plants have an economic value, although no case studies have yet estimated it (Green and Elmberg 2014). One potential way of valuing part of the dispersal service by waterbirds would be to calculate the replacement costs of manually planting the wetland plant species that become established in and around created or restored wetlands after arriving via birds; those costs alone would be extremely high. In addition, the costs of replacing dikes that are vital in preventing floods, or in containing water in fish ponds, and which are protected from wave erosion by vegetation brought by birds, should be estimated. Recent progress in accounting for ecosystem services provided by migratory species (Semmens

et al. 2011) is relevant, since many migratory waterbirds that provide dispersal services cross international borders. For example, ducks dispersing plant diaspores to new habitats in the United States breed largely in Canada. The valuation of such dispersal services by waterbirds is an important avenue for future research (Green and Elmberg 2014). However, to facilitate such valuation, much basic research is still needed to improve our understanding of which plants are dispersed by waterbirds, and where.

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