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Long-distance endozoochorous dispersal of submerged macrophyte seeds by migratory waterbirds in northern Europe—a critical review of possibilities and limitations

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Abstract

We review whether migratory Anatidae, i.e., swans, geese and ducks, could be acting as vectors for dispersal of *Zostera*, *Ruppia* and *Potamogeton* propagules by endozoochory (carrying seeds in their guts). We list six prerequisites that must all be fulfilled, if successful dispersal should occur. Several Anatidae species feed on these macrophytes, and undertake rapid long-distance movements, making dispersal possible. We identify four problems, which in combination leads us to conclude that long-distance dispersal events are likely to be rare. (i) Most long-distance movements are out of phase with the reproductive efforts of the plants, and if birds arrive at sites when plants still bear seeds, they are likely to depart well after seed stocks have been depleted. (ii) Seed transport by birds will usually be uni-directional, from north to south on autumn migrations. (iii) Most of the gut contents of migratory birds are likely to have been discarded within 300 km of departure. (iv) In many cases, birds will arrive in habitats seriously different from those they departed, i.e., any seeds carried along will have low chances of surviving in their new site. We suggest that northbound dispersal by endozoochory can only occur during spring if waterbirds feed on seeds that have not been depleted and remained frozen down or buried in sediments, or during moult- or post-moult migrations. Moult migration takes place in summer in phase with the reproductive efforts of the plants. Also epizoochorous dispersal (external attachment) is subject to restrictions i, ii and iv.

Keywords: Anas; Branta; Cygnus; Potamogeton; Ruppia; Zostera

1. Introduction

Within a few years of their creation, lakes and other wetland habitats flourish with life at all trophic levels, ranging from tiny unicellular algae and zooplankton to large fish- and plant-eating waterbirds and mammals. How this colonisation of pristine wetlands, especially those isolated from other wetlands, takes place already puzzled Darwin (1859), who is often quoted as the first author to suggest that birds move propagules of aquatic organisms between lakes. The dispersive potential of waterbirds is beyond doubt: they are highly mobile, and regularly move between local wetlands. Waterbirds, more than any other group of organisms, migrate over long distances, and are the most obvious candidates for vectors of long-distance dispersal. Some organisms might also be water- or wind-dispersed, but birds remain the major candidates for dispersal of several types of organisms, ranging in size from ostracods to aquatic macrophytes. Small snails have been found adhering to bird feathers (Vagvolgyi, 1975), and seeds from bird feathers and in the mud adhered to birds' feet have been successfully germinated (Wallace, 1895). Propagules externally attached to the feathers, bills and legs of waterbirds and carried to other sites is therefore one possible means of dispersal (epizoochory). An alternative method is that of gut-mediated dispersal (endozoochory) of propagules ingested by plant-eating waterbirds. This requires a proportion of the ingested propagules passing undigested through the guts of the birds, or at least being so weakly digested that they emerge still capable of germination after passage. If the

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birds have moved from the original site of ingestion, the propagules will be ejected in the faeces the birds produce in a new site.

Dispersal of plant propagules by birds over short (0–100 m) to medium (100–20,000 m) distances have frequently been recorded in terrestrial plants (e.g., Wenny and Levey, 1998; Holbrook and Smith, 2000). In a recent review of the existing record on dispersal of aquatic organisms by waterbirds, Figuerola and Green (2002) concluded that there was ample evidence for transport of viable organisms at a local scale. However, long-distance dispersal (20–1000 km or more) is generally believed to be a rare event, although there is no quantification of how rare it actually is (Cain et al., 2000). Long-distance dispersal might be expected to be more common in aquatic than terrestrial plants, especially because many waterbird species feeding on aquatic plants generally migrate over longer distances than do most frugivorous or granivorous passerines. Figuerola and Green (2002) stated that long-distance dispersal of propagules was possible given the recorded survival of the digestion process, maximum retention times of the propagules and flight times of the birds, but that the frequency of such long-distance dispersal events remained unknown. Colonisation of Australia and Tasmania by aquatic plants shows that long-distance dispersal, presumably by birds, must have taken place in historical times (Jacobs and Wilson, 1996; Jordan, 2001). The question then is to what extent migratory waterbirds facilitate long-distance dispersal of aquatic plants, and how they might have contributed to the post-glacial establishment of submerged macrophyte populations, so widely distributed over the northern hemisphere (Santamaría, 2002)?

In this paper we focus on gut-mediated dispersal of seeds from a specific group of aquatic plants—submerged macrophytes, which are abundant and highly productive primary producers in lakes, brackish and saline wetlands throughout the world (Thayer et al., 1984; Kantrud, 1990, 1991). Due to their abundance, several herbivorous waterbirds feed on these macrophytes, and could potentially act as important vectors for dispersal (Cook, 1987). We do not consider dispersal of other propagules than seeds such as *Potamogeton* tubers or *Vallisneria* turions, although they are important food items for a number of waterfowl species such as tundra swans (*Cygnus columbianus*), canvasbacks (*Aythya valisineria*), pochards (*Aythya ferina*), and red-crested pochards (*Netta rufina*) (Brouwer and Tinbergen, 1939; Cramp and Simmons, 1977; Perry and Uhler, 1988; Hohman et al., 1990). This is because these starch-rich structures are probably digested to an extent (see Nolet and Drent, 1998) that they will not sprout after passage through the gut.

We do not intend to review the global literature on dispersal of aquatic plants by waterbirds—partly because Figuerola and Green (2002) already did this. Our intention is to outline constraints and limitations that we believe exist to gut-mediated dispersal of seeds from aquatic macrophytes by birds, some of which have been overlooked. We use examples from studies of waterbirds feeding on three major groups of submerged macrophytes, eel-grasses (*Zosteraceae*), pond-weeds (*Potamogetonaceae*), and tassel-weeds (*Ruppiacea*). Judged from the existing, mainly anecdotal, literature reporting on avian herbivory on submerged macrophytes, these groups represent one of the most important food sources taken by waterbirds. We concentrate on a few well-studied species of waterbirds from northern Europe that feed on these plants, and use these as examples to address several prerequisites, which must be fulfilled for gut-mediated long-distance dispersal of seeds by birds to take place. These prerequisites are:

- food selection: birds must feed on the seeds of aquatic macrophytes;
- timing: to harvest and carry seeds onwards, their availability must coincide with the period when the birds are about to leave a given site for another;
- non-starving: to be able to carry seeds along, birds must fly with their guts at least partly filled;
- rapid movement: assuming that digestion of seeds will continue during migratory flight, birds must move rapidly between sites if seeds are to survive the journey;
- retention time: to achieve long-distance transport the seeds must be retained long enough in the birds' guts;
- linkages between appropriate habitats: birds moving from one site to another must eject ingested seeds in appropriate habitats upon arrival.

We address each of the above prerequisites, but will not explicitly consider the capability of the seed to sprout after passage through the gut, or the subsequent establishment of the seedling. These issues are, of course, fundamental to successful long-distance dispersal, but have been addressed elsewhere (e.g., Figuerola and Green, 2002; Charalambidou and Santamaría, 2002).

2. Birds feeding on seeds from aquatic macrophytes

The first prerequisite enabling endozoochorous dispersal of seeds from submerged aquatic macrophytes by birds to take place is that birds feed on these. Figuorola and Green (2002) pointed out that waterfowl Anatidae are amongst the most likely potential dispersive agents of aquatic macrophytes, and we believe this certainly holds true for northern Europe. The coot (*Fulica atra*) is the only non-Anatidae waterbird that is numerous, (partly) herbivorous, and feeding on submerged plants (Cramp and Simmons, 1980). The Anatidae show a remarkable degree of adaptive radiation that enables exploitation of highly seasonal food resources separated in time and space. The majority of the European Anatidae species undertake long-distance migrations from arctic or northern temperate breeding sites, in Fennoscandia, Russia and Siberia to southern temperate, sub-tropical or even tropical wintering areas in south or western Europe and north or western Africa. Most species accumulate energy stores, which can fuel these long distance flights, and several do this by feeding on leaves and seeds of aquatic plants. These feeding habits, in combination with their highly migratory habit, make waterfowl the primary candidates for the long-distance dispersal of aquatic macrophyte seeds.

The most obvious candidates as dispersers of seeds are those that feed specifically on these, either by taking them directly from the plants, or by filter-feeding in bottom substrates. In the western Palearctic, for example, teal (*Anas crecca*) feed on a range of seeds of aquatic macrophytes such as *Potamogeton*, *Ruppia* and *Myriophyllum* (Cramp and Simmons, 1977). The slightly larger pintail (*Anas acuta*) feeds in brackish and marine environments and is more an animal feeder, although it also feeds on the seeds and tubers of *Potamogeton*, and seeds of *Ruppia* where these are abundant (Spärck, 1958; Cramp and Simmons, 1977). Mallard (*Anas platyrhynchos*), a highly omnivorous species, likewise occasionally feeds on seeds of macrophytes including *Potamogeton* (Cramp and Simmons, 1977). The Eurasian wigeon (*Anas penelope*) primarily grazes the green parts of aquatic macrophytes, but also quite frequently takes seeds of *Potamogeton* and *Ruppia* (Spärck, 1958; Cramp and Simmons, 1977). A few specialist Anatidae forms exploit submerged macrophytes by diving. In particular, the omnivorous pochard, often exploits seeds of aquatic plants, especially *Potamogeton*, *Zannichellia*, *Zostera*, and *Ruppia* (Cramp and Simmons, 1977). The red-crested pochard, although mainly a *Chara* specialist, occasionally feeds on seeds of, for instance, *Potamogeton* (Cramp and Simmons, 1977).

Some birds feed primarily upon green plant parts, but in so doing, unintentionally ingest seeds, and so may also be potential candidates to transport reproductive plant parts. The largely sedentary mute swan (*Cygnus olor*), for example, feeds on the green parts of a range of submerged macrophytes in freshwater, brackish and saltwater habitats, including *Chara*, *Zostera*, *Ruppia*, *Potamogeton*, *Najas*, and *Zannichellia*. Whooper swans (*Cygnus cygnus*) preparing for migration from the Pechora Delta in sub-arctic Russia were observed feeding on *Potamogeton perfoliatus* leaves, and faeces collected contained seeds from the plants (M. Klaassen, unpublished). Bewick's swans (*Cygnus columbianus bewickii*) feeding in the same area probably did the same, but sampling of their droppings was not possible. Wintering whooper swans also fed on green parts of submerged macrophytes (*Ruppia*, *Potamogeton* and *Zostera*) in Danish coastal areas in the 1950s–1970s (Spärck, 1958; Joensen, 1974) prior to the more recent shift to agricultural habitats. Whilst most goose species are generally grazers of graminoid plants outside of the breeding season, the brent geese (*Branta bernicla*) of the northern hemisphere stand out as exceptions to this rule, feeding on inter-tidal or sub-littoral *Zostera* beds throughout much of its global non-breeding range (Ganter, 2000).

3. Timing of seed production of aquatic macrophytes and foraging waterbirds

The second prerequisite for endozoochorous seed dispersal by birds is that the foraging waterfowl must be able to harvest the ripened seeds at the time they are about to depart for remote areas.

This criteria may, however, be rarely met in reality, as exemplified by brent geese feeding on seagrasses of the genus *Zostera*. Reproduction amongst the sub-littoral *Zostera marina* populations studied throughout the world is largely asexual, so vegetative parts of plants dominate the food available to the grazers. If reproduction takes place, flowering starts during April–May, and the reproductive (i.e., seed-carrying) plants are only numerous during June–September, although some can still be found in December (Sand-Jensen, 1975; Wium-Andersen and Borum, 1984; Olesen and Sand-Jensen, 1994). Inter-tidal *Zostera* species such as *Z. noltii* invest more in sexual reproduction, but the vegetative shoots still constitute the majority of biomass, and most reproductive shoots have disappeared by the end of September (Philippart, 1995). Thus, the phenology of reproduction of *Zostera* spp. is poorly matched with that of the migrating brent geese (Fig. 1). The light-bellied brent geese (*Branta bernicla hrota*) from Svalbard and Greenland migrates to the wintering areas during early–mid September and departs towards the breeding areas in the last week of May (Clausen et al., 1998). The dark-bellied brent geese (*Branta bernicla bernicla*) arrive to winter in western Europe in mid–late September and depart in mid–late May. In autumn, they spend most of their feeding time on inter-tidal *Zostera noltii* and *Z. angustifolia* and sub-tidal *Z. marina* beds in the Danish–German–Dutch Wadden Sea, UK and France, before they switch to feeding on inter-tidal beds of algae (*Enteromorpha*), saltmarshes or agricultural habitats in mid-winter (Ranwell and Downing, 1959; Tubbs and Tubbs, 1982; Prokosch, 1984; Maheo and Denis, 1987; Madsen, 1988).

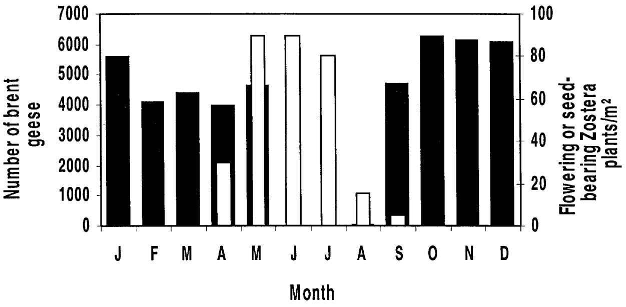

Fig. 1. Phenological mismatch between reproduction of *Zostera marina* and brent geese feeding on *Zostera* plants. The phenology of the brent geese is given with black bars, which indicate the average of monthly maxima of light-bellied brent geese counted during the wintering seasons 1992/93–1994/95, derived from Clausen et al. (1998). The white bars give the average number of reproductive *Zostera marina* plants/m^2 in a Danish study (from Olesen and Sand-Jensen, 1994).

Thus, most brent geese from these two populations are likely to spend most of their feeding outside the main season for sexual reproduction of the plants. They will feed largely upon vegetative *Zostera* plants and depart at the time when there are fewest sexual propagules in the accessible environment. Even if brent geese would feed on the few *Zostera* plants still bearing seeds upon arrival, they will not leave the area until long after all the seed-carrying plants have disappeared. The brent geese only depart from the *Zostera* beds after depleting the vegetative shoots to low biomass densities (Jacobs et al., 1981; Tubbs and Tubbs, 1983), and quite frequently after spending some additional time digging for below-ground plant rhizomes (e.g., Madsen, 1988).

The mismatch between the phenology of reproduction of *Zostera* and the grazing brent geese may not be so prevalent amongst the slightly earlier migrating populations of dabbling ducks, such as teal or wigeon arriving in September to their western European autumn staging areas. Their earlier arrival enables access to ripe seeds attached or already shed from the submerged macrophytes. These species also feed on seeds from plants such as *Ruppia* spp. and *Potamogeton* spp., which invest relatively more in sexual reproduction and store more nutrients in seeds than *Zostera* spp. (e.g., Kantrud, 1990, 1991). Despite this match in phenology, the seeds may already be depleted before the migrants arrive. In the Lauwersmeer, the Netherlands, *Potamogeton pectinatus* produces seeds in July. Based on exclosure experiments, it was shown that moulting dabbling ducks, mainly mallards, consumed c. 95% of the seeds (L. Santamaría, unpublished). By the time the long-distance migrants (teal, pintail, wigeon) arrive on the scene in September, the majority of seeds are gone. Madsen (1988) found that both wigeon and teal fed on a *Zostera noltii* bed immediately upon arrival to the Wadden Sea in September–early October. However, prior to their continued migration both species switched to feeding on seeds from salt marsh plants.

One potentially important example where the plants and the grazers are much more likely to match in time and their interaction may result in dispersal is that of waterfowl on moult migration. For example, mute swans are widely distributed breeders in lakes and brackish coastal areas throughout most of the Baltic Sea (Cramp and Simmons, 1977). Non-breeding birds (failed breeders and immature birds) migrate to safe non-breeding habitats with large food supplies where they moult their flight-feathers, remaining flightless for approximately 7 weeks, during July–August. Most birds from this population move to moulting sites in the western parts of the Baltic Sea, i.e., south-east Denmark, southern Sweden, north-east Germany (Andersen-Harild, 1971). After moult, most birds disperse away from the moulting sites, many returning to their sites of origin in the eastern Baltic, i.e., Poland, Latvia, Lithuania and Estonia (Andersen-Harild, 1981). This return migration occurs when the birds have potentially ingested the seeds of the submerged macrophytes they feed on, e.g., *Zostera marina*, *Potamogeton pectinatus*, *Zannichellia* spp., and *Ruppia* spp. (Mathiasson, 1973; P. Clausen unpublished).

In contrast with all the evidence listed above, the majority of Bewick's swans in the Pechora Delta in northern Russia, prepare for autumn migration by feeding on tubers, but also leaves and seeds, of *Potamogeton pectinatus* and *Potamogeton perfoliatus*. Seeds are still abundant on the food plants in late September, after the swans have departed (M. Klaassen, unpublished). These swans are therefore most likely to carry seeds along on their return migration from their sub-arctic breeding or moulting sites.

4. Are waterfowl feeding prior to long-distance migrations or do they fly without guts?

The third prerequisite for endozoochorous seed-dispersal by birds is that waterfowl must be feeding up to the point of departure from a feeding site. Studies of eared grebes (*Podiceps nigricollis*) and several species of waders show that, prior to long-distance migrations, these birds reduce the size of their digestive organs (e.g., Jehl, 1997; Piersma and Lindström, 1997; Piersma and Gill, 1998). This atrophy of the alimentary tract is believed to have two purposes. Firstly, by travelling 'without guts' the birds reduce flight costs. Secondly, the birds use the nutrients mobilised by catabolism of the digestive system to build larger pectoral muscles, thereby improving their flight capabilities during the long-distance journeys. It is now also documented that these changes can occur within a few days (Gaunt et al., 1990; Piersma et al., 1999). The drawback, however, is that waders with smaller stomachs are restricted to a diet based on relatively soft food items (Piersma et al., 1993). It is generally considered that birds feeding on 'soft-shelled' invertebrates have smaller gizzards, shorter intestines and smaller cecae than birds feeding on seeds or plant materials. The latter need larger gizzards for grinding food of high fibre content, which also demands longer intestines and larger cecae to be digested (see reviews by Clench and Matthias, 1995; MacWilliams and Karasov, 2001).

Annual changes in the size of the alimentary tract of waterfowl are known to take place. Breeding birds may use body protein (especially those of the gizzard) for egg-formation or metabolism during incubation (e.g., Krapu, 1981; Ankney and Alisauskas, 1991; Mann and Sedinger, 1993). In waterfowl gut structure may change in response to dietary changes within relatively short time frames (e.g., Miller, 1975; Kehoe et al., 1988; Moorman et al., 1992). Unfortunately, however, it is not known whether similar changes in the intestinal system of waterfowl occur in preparation for long-distance migrations, in line with changes observed in waders and grebes. If we are to better understand the potential of waterfowl as dispersal vectors of aquatic macrophytes, improving our knowledge on this subject is essential. Pre-migratory changes in gut morphology, and especially gizzard atrophy, might force omnivorous birds to switch from feeding on seeds to feeding on invertebrates if available. Consequently, strict herbivores would have to stop feeding all together, a few days prior to departure. It is obvious that such pre-migratory preparations would restrict dispersal possibilities. However, although observations on waterfowl foraging behaviour just prior to migration are rare, there is little evidence of any reduction in their foraging intensity.

During spring in the White Sea, Russia, Bewick's swans on their last major stopover site on their way to the breeding grounds only feed during low tide and rest during high tide (Nolet and Drent, 1998). Of 18 groups that were observed departing for their last stretch of the migration between 19 and 28 May 1996, 28% left within the first hour after they had stopped foraging, as defined in Nolet and Drent (1998) (Fig. 2), i.e., 3.3 times more than expected by chance. The majority of the swans thus left directly after a foraging period. Also observations in the Pechora Delta of the same species do not support the idea of a total cessation of foraging prior to departure. Prior to the massive departure of swans from this area on 25 and 26 September 1998, which left the area almost completely void of swans, most swans in the area were observed foraging. The last count in the census area on 23 September comprised 863 swans foraging and none resting. Over the pre-migratory period daily counts were made in the census area from 10–12 and 14–23 September, counting 708 swans of which on average 15% were resting (M. Klaassen, unpublished).

These observations suggest that herbivorous waterbirds may be more likely to initiate migratory movements without a preceding starvation period than are some wader species.

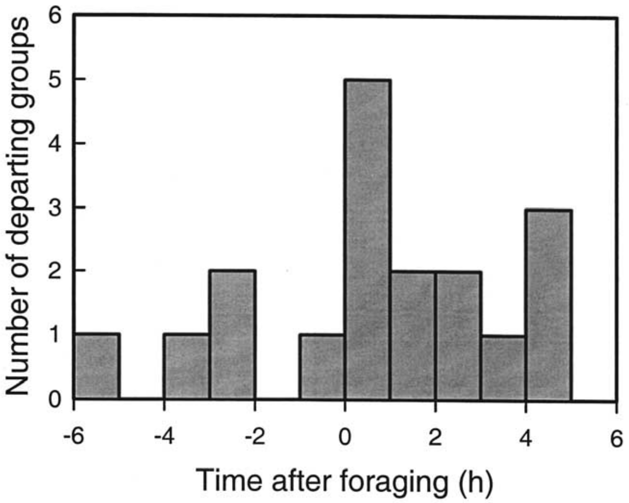

Fig. 2. Number of departing groups of Bewick's swans in the Dry Sea (White Sea, Russia) in May 1996 in relation to the time the swans stopped foraging due to high water levels during high tide. A group departing within a negative hour period thus left the site before the swans in the area generally stopped foraging.

5. Evidence of fast movements between sites

The fourth prerequisite for endozoochorous seed-dispersal by birds is that the grazing waterfowl must move rapidly between sites, reducing the digestion risk to the transported propagule.

Long-distance movements performed by some of the brent goose populations have recently been followed by satellite telemetry, and results from these studies confirm that waterfowl can move over quite substantial distances within short periods. Clausen and Bustnes (1998) tracked light-bellied brent geese on spring migration from Denmark to Svalbard and Greenland (Fig. 3), which flew 2600–3500 km in less than 94 h. Dark-bellied brent geese, tracked with the same method from the Wadden Sea to the Taimyr Peninsula in Siberia (M. Green et al., 2002a) (Fig. 3), made their first almost non-stop flight from the Wadden Sea to the White Sea covering 2300 km in less than 96 h.

Teal captured and ringed during their autumn staging in Denmark continue south-westwards in the course of the year and are mainly recovered during the winter in Ireland, Britain, western France and Spain (A.D. Fox and I. Clausager, unpublished). Amongst 6965 subsequent reports of teal captured and ringed in Denmark between 1949 and 1983, there were a few instances of very rapid movements. Thirty-one individuals moved more than an average of 100 km per day between the dates of marking and recovery (Fig. 4). Such calculations underestimate the potential speed of the flight since released marked birds are unlikely to depart immediately after release from capture, and the time of recovery is unlikely to correspond to the point of arrival. Nevertheless, it appears that teal can potentially move 1000 km in a few days without difficulty, and one individual caught during 1997 in particular is known to have migrated 1285 km within 24 h (Fig. 4).

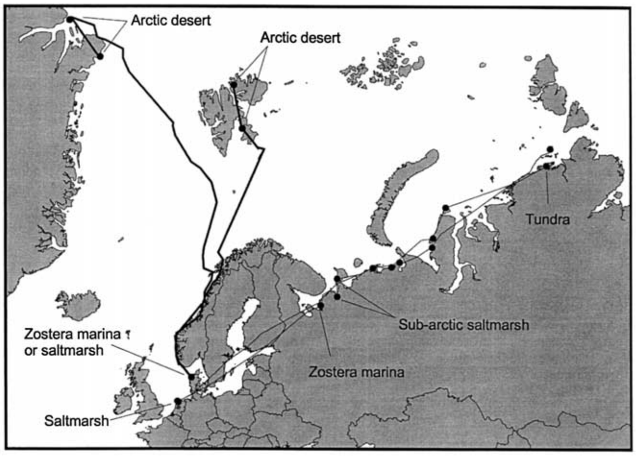

Fig. 3. Examples of long-distance trackings of light-bellied brent geese (thick lines) and dark-bellied brent geese (thin lines), and habitat use of the geese en route during spring migration to the breeding grounds. Dots give staging areas used by the birds. Tracks are redrawn from Clausen and Bustnes (1998) and M. Green et al. (2002a), and the habitat use account is based on a literature review.

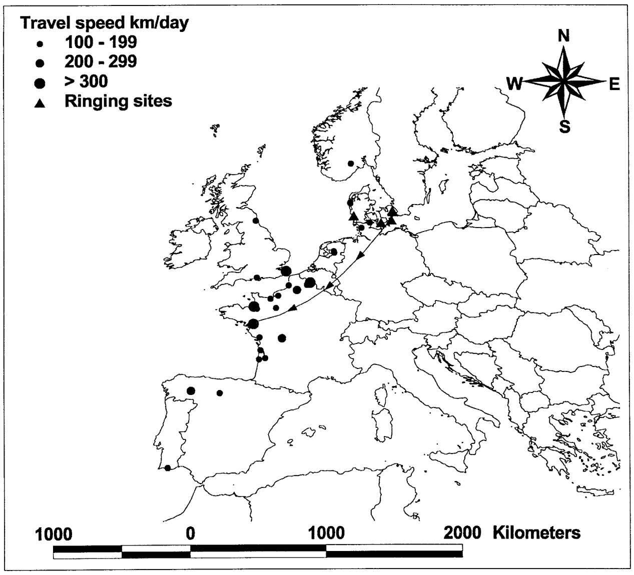

Fig. 4. Distribution of direct recoveries (dots) of Danish ringed teal marked at four capture sites (triangles) 1949–2000, and moving more than 100 km per day during the period between capture and recovery. The size of the dots gives a range of minimum distances moved per day. All individuals were ringed between 1 July and 31 December and recovered shot, found dead or recaptured between 1 July and 1 March of the same wintering season. The arrow highlights the movement of one individual teal from Denmark to France within 24 h. This was a radio-tagged adult female marked on Tyreholm on 4 December 1997, still present at the site on 5 December at 16.00 hours (radio fix), which was shot in western France, 1285 km (orthodromic distance) away on 6 December 1997, precise time unknown. If the bird departed immediately after its last radio detection in Denmark and was shot on the morning flight (c. 08.00 hours) this represents an average speed of 80.3 km h^{-1} if shot on the evening flight (17.00 hours), this would represent 51.4 km h^{-1}.

We have no information on migratory performance of pintails from Europe, the potentially longest migrating duck breeding in northern Europe. Data from pintail migrating northwards in spring up the Pacific flyway of the United States, however, offer a source of long-distance migration speeds. Satellite telemetry has provided detailed information on the individual trajectories of female pintails tagged in California and followed to the breeding areas in spring (Miller et al., 2000). Data from two birds with multiple up-link locations over the Pacific Ocean between north-eastern California/southern Oregon and Alaska enabled flight speed calculations for part of this journey. The mean speed from these measurements was 70 km h^{-1}, at which a Pintail could potentially cover 1680 km in 24 h. It is therefore possible that the birds, which were recorded migrating from California/Oregon to Alaska (2300–2800 km) could do so in a single flight of 33–40 h (M.R. Miller, personal communication), although these birds might also land on the open sea to rest periodically.

Non-stop flights of five Bewick's swans tracked by satellite on their autumn migration after departure from the Pechora Delta in sub-arctic Russia ranged between 700 and 1600 km, measured as great circle distances, with durations of between 11 and 23 h. During spring migration from western Europe, 13 tracked swans flew 150–600 km from one stopover to the next (J.H. Beekman, unpublished). This finding corresponds well with results from 12 North American tundra swans that were also tracked by satellite. While migrating between wintering areas and prairie staging areas in spring, individual movements were generally less than 500 km. However, movements from the final spring staging areas to the breeding grounds were generally much longer. One bird travelled 1900 km non-stop between northern Saskatchewan and the Mackenzie River Delta (S.A. Petrie and K.L. Wilcox, unpublished).

6. Long-distance migrations and physiological limitations on dispersal

The question relevant to the gut-mediated dispersal of propagules is, however, whether such long-distance movements over short periods also means that the birds arrive at new habitats having retained undigested propagules in their guts.

As mentioned earlier, herbivorous birds generally have longer intestines and cecae compared to, e.g., piscivorous or insectivorous birds. Within herbivorous birds, however, there is also large variation in the size of the alimentary tract. Herbivorous waterfowl have considerably smaller cecae than herbivorous grouse Tetraonidae (Sedinger, 1997). The exact function of the cecae is disputed (Vispo and Karasov, 1997), but Sedinger (1997) points out that the consequence of the difference between grouse and waterfowl is that the latter have a relatively lower digestive capacity than grouse, which they cope with by eating relatively large amounts of food that is processed rapidly and ejected after poor digestion. This means that, on the one hand, the ingested propagules have a 'lower risk of being digested' if eaten by waterfowl, but on the other hand will be ejected relatively soon after ingestion.

Studies of a passerine bird regularly flying 12 h in a wind tunnel showed that at least some birds produce droppings while flying, and not only shortly after take-off (Klaassen et al., 2000). How far a seed is potentially carried inside the gut of a bird thus depends not only on how far a bird can fly but also on how far a propagule will be carried in the migrant's gut. We addressed this question in detail in Appendix 1, where we made a compilation of observed flight speeds of waterfowl. We subsequently used an allometric relationship that describes the amount of energy reserves a bird can maximally carry during flight as a proportion of its body mass from data compiled by Hedenstöm and Alerstam (1992). Dividing the energy reserves by the flight costs (per unit distance) from aerodynamic theory or, alternatively, an allometric relationship, gives the maximum distance a bird can fly. Alternatively, we used data on the average length of time plant food is retained in the gut of waterfowl (Bruinzeel et al., 1997). Multiplied by the observed flight speeds, this gives the distance over which endozoochorous transport can take place. The analysis suggests that the maximum distance a waterfowl can fly without refuelling stops is in the order of 2000–5000 km (Fig. 5). The average distance over which the bulk of ingested propagules would be transported increases with body mass from teal (0.3 kg) to mute swan (10.8 kg) due to the longer retention time and greater flight speeds in large birds, but it remains an order of magnitude less than the maximum flight distance, in the range of 100–500 km (Fig. 5). This means that the majority of the propagules are probably ejected long before the final destination of a long-distance flight has been reached.

7. Linkages between appropriate habitats for dispersal

Assuming that a bird will reach a new site after a migration move and, despite all the limitations pointed out in the previous paragraphs, will eject some seeds from its previous staging site with its faeces, the next prerequisite is that the habitat characteristics of the new site match those of the site it departed from.

Bewick's swans heavily rely on *Potamogeton pectinatus* during both spring and autumn migration (Beekman et al., 1991). As such they tend to visit similar habitats again and again. However, Bewick's swans seem to be an exception when compared with many other species of north European waterfowl, such as brent goose, wigeon and pintail.

The Svalbard and Greenland light-bellied brent geese winter in nine sites, eight in Denmark and one in England, and four of these have only recently been occupied (Clausen et al., 1998, 1999). At two of these sites, the Danish Wadden Sea and Lindisfarne, the birds feed on *Zostera noltii* and *Z. angustifolia* on inter-tidal mudflats, whereas in the remaining sites they feed on sub-tidal *Z. marina* beds in areas with little tidal amplitude (Percival and Evans, 1997; Clausen and Percival, 1998). The phenology of site-use has changed dramatically since the second half of the 1980s (Clausen et al., 1998), but prior to that period the whole population arrived to the Wadden Sea in early September and dispersed from there to Mariager–Randers Fjords and Lindisfarne during November–December. It was, however, less than a quarter of the birds that moved to Lindisfarne, the site of comparable habitat signature (Owen et al., 1986; Clausen et al., 1998). This example is based on a small population with a limited range, and other populations might indeed be moving much more between appropriate habitats for dispersal. For example in autumn, dark-bellied brent geese in western Europe migrate between several sites where they feed on *Zostera noltii* and *Z. angustifolia* on inter-tidal mudflats (e.g., Tubbs and Tubbs, 1982; Prokosch, 1984; Maheo and Denis, 1987; Madsen, 1988; Fox, 1996).

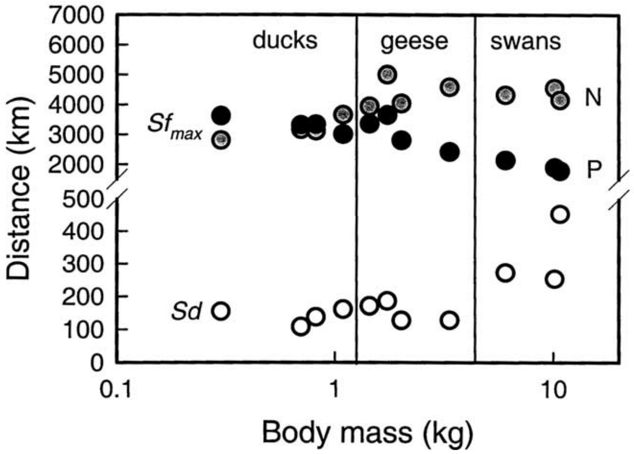

Fig. 5. Plot of calculated maximum flight distance Sf_{max} (black and grey dots) and potential mean dispersal distance Sd (white dots) against body mass. Black dots marked with P are maximum flight distances estimated using aerodynamic theory, based on Pennycuick (1989) with modifications. Grey dots marked with N are maximum flight distances based on an allometric relationship (Norberg, 1996). Details on calculations are given in Appendix 1.

Pintail staging in Danish Baltic wetlands during autumn feed on the seeds of brackish water plants, especially *Ruppia* (e.g., Spärck, 1958), and wigeon staging in the same areas largely feed on leaves of *Ruppia*, *Potamogeton* and *Zostera marina* and on seeds of *Potamogeton pectinatus* (Madsen et al., 1992). It is therefore worth concentrating upon the potential for birds feeding on the abundant autumn seed fall stock of submerged macrophytes in Danish Baltic wetlands, to disperse seeds to wintering habitats of these birds further west in Europe.

Very few pintail and wigeon have been ringed in these Danish areas. A comparison of phenology curves of occurrence in the inner Danish waters, where birds arrive in September and numbers peak in October (Joensen, 1974), with those further west, with peaks in numbers both in the Netherlands and in UK during mid-winter (SOVON, 1987; Owen et al., 1986), suggest that the same birds may be involved. Owen and Mitchell (1988) analysed recoveries of 1419 wigeon ringed in the UK and recovered abroad, and of 401 birds ringed abroad and recovered in the UK. They found that the median recovery locations of both females and males were in Denmark during October, the males having arrived to Denmark already in September, whereas females were found further east in Finland that month. Both sexes from Denmark probably continue to winter in the south of the UK during November–February.

However, this wide-scale movement amongst two numerous dabbling duck species gives little opportunity for the successful spread of seeds to suitable habitats. From Baltic staging areas, pintail and wigeon move to staging areas in the Wadden Sea and to Britain and Ireland. Pintail in these areas have highly aggregated coastal winter distributions and are specialist feeders, feeding either on seeds of salt marsh plants or on the mollusc *Hydrobia ulvae* in intertidal areas (de Vries, 1939; Cramp and Simmons, 1977). Wigeon in the same areas generally feed on intertidal *Zostera noltii* and *Z. angustifolia* beds, before switching to seeds from saltmarsh plants or improved grasslands (Owen, 1973; Madsen, 1988).

On this basis, plant parts carried from Baltic submerged brackish and freshwater macrophytes by pintail or wigeon would be highly unlikely to encounter suitable settlement conditions in the habitats used subsequently by these species in the Wadden Sea or in the UK and Ireland in late autumn and mid-winter. For example, *Ruppia spiralis* and *R. maritima* are described as rather rare and local in Britain and Ireland (Clapham et al., 1987). Both are confined to brackish lagoons, which are the subject of a current habitat biodiversity action plan in the UK because of their rarity and fragility, yet both species are common and widespread in Baltic wetlands.

The low probability for seeds to be dispersed to suitable habitat by waterfowl migrating from the wintering habitats becomes even more apparent when addressing the potential for very long-distance dispersal. This is highlighted by satellite tracking of brent geese (Fig. 3) combined with ground-based information on food selection in the departure and destination locations. The light-bellied brent geese migrating from Denmark to the Arctic moved from a spring staging area where they feed on *Zostera marina* and saltmarsh plants (Clausen, 1998) to breeding areas in Svalbard and Greenland where they feed on a variety of arctic graminoids and dicotyledonous plants (Nyholm, 1965; Hjort et al., 1987; Madsen et al., 1989). The dark-bellied brent geese divide their spring migration into three flights; the first almost non-stop from the Wadden Sea to the White Sea; the second from the White Sea to the Kanin Peninsula; and the third from Kanin to Taimyr. In the Wadden Sea, the birds mainly feed on graminoids in saltmarshes (e.g., Boudewijn, 1984; Prop and Deerenberg, 1991); in the White Sea, they feed on *Zostera marina* (Clausen, 1997); on Kanin, they feed on sub-arctic saltmarsh graminoids (Filchagov and Leonovich, 1992; R.H. Drent, unpublished); and in Taimyr, on arctic tundra graminoids and dicots (Spilling and Stock, 1995).

8. Discussion

In this paper, we have tried to shed some light on a number of factors that may constrain on long-distance endozoochorous seed dispersal by migratory waterfowl. On the basis of our examples, taken from northern European migratory Anatidae populations, it is tempting to conclude that long-distance dispersal is rare, because many of the six listed steps—or prerequisites—seem to limit the chance for a successful dispersal event.

In a recent review of the existing record on dispersal of aquatic organisms by waterbirds, Figuerola and Green (2002) already identified Anatidae as the major potential disperser group. However, the submerged macrophytes we considered bear seeds in summer rather than in the peak migratory period of waterbirds in autumn. This mismatch in timing between the two impairs long-distance dispersal, except in the mentioned examples of moulting swans from the Baltic and Pechora Delta. In addition, waterfowl might be flying with empty or reduced digestive systems, as has been shown in grebes, waders and passerines. However, evidence is lacking and field observations suggest that at least swans do not fast just prior to long-distance migrations. If the waterbirds depart with full guts and move rapidly, the distance over which dispersal may occur is still limited by the food retention time. The majority of seeds are probably ejected while the birds are in flight, and these seeds most likely will end up in unsuitable habitat in between wetlands. A.J. Green et al. (2002) point out that even though the majority of seeds may have left the birds when they arrive, those few that still are trapped in the intestinal system of the birds may be representing rare but important dispersal events. A.J. Green et al. (2002) consider therefore that migratory or nomadic movements of ducks are likely to be of major importance to plant population connectivity in Mediterranean and tropical wetlands.

We do not exclude the importance of such rare events, but from our analysis it is tempting to conclude that in more northerly regions seeds will only occasionally be successfully transported over considerable distances to a suitable habitat. Some of the examples of long-distance migrations that we give are based on spring migration events, but there are good reasons to believe that the birds use more or less the same sites during spring and autumn. This is evidenced from the dark-bellied brent geese tracked in both directions (compare M. Green et al., 2002a, b), and from trackings of Bewick's swans in both directions (J.H. Beekman, unpublished). Even if the seeds are carried all the way to the next stopover during a long-distance flight, the habitat is often very different from the original one, possibly hampering establishment.

Infrequent dispersal may create a negative feedback by which successful dispersal becomes even more rare. When the gene flow between plant populations is low, these populations will gradually become genetically differentiated (Ouborg et al., 1999). If this differentiation has a significant adaptive component, local adaptation might arise, as exemplified by local speciation in genera such as *Nymphoides*, *Utricularia*, *Nymphaea* and *Vallisneria* in Australia (Jacobs and Wilson, 1996). Local adaptation processes would make successful establishment of the less adapted immigrants increasingly unlikely, further enhancing the genetic differentiation of the plant populations and hampering future establishment (see De Meester et al., 2002, for a discussion of the constraints on effective dispersal posed by local adaptation).

This argument only holds when the plants have already colonised the wetlands along the migratory route. Colonisation of virgin habitat is not constrained by plant competition, and rare dispersal events may be of great significance in the spreading of plant populations. This might conversely mean that the gene flow caused by present day dispersal only plays a very minor role in comparison to past events.

Mader et al. (1998) found evidence for long-distance dispersal of *Potamogeton pectinatus* by migratory birds. They detected a stronger correlation between geographic distance and genetic distance among sites not visited by Bewick's swans than among stopover sites of these birds. In addition, some members of the most northerly population of *Potamogeton pectinatus* used by the swans, in the Pechora Delta, were closely related to central and western European populations, based on chloroplast markers, whereas other members in the Pechora Delta were very different. From these findings, they inferred that seed transport by Bewick's swans or other migratory birds using the same migration trajectory had resulted in successful establishment of plants along this route. How long ago this establishment took place is unclear.

This raises another interesting question. Our current notion is that seed transport by birds will usually be uni-directional, taking place from north to south on autumn migrations. In this light, it is difficult to imagine that virgin habitat, which was created after retreat of the glaciers at the end of the last ice-age has been colonised through endozoochorous transport of seeds. After all, it would imply birds flying northwards during the autumn migration (after fattening up on seeds).

Northward dispersal may possibly arise from tuber-digging swans or filter-feeding dabbling ducks in spring, which intentionally or accidentally, feed on seeds that have been frozen down in northerly staging areas during the winter or lay on the sediment's surface. However, our knowledge about such events is limited because most studies on the feeding ecology and nutrition of Anatidae seldomly have been conducted during spring. Another possibility for northward dispersal is during moult migration, and in particular during post-moult migration. Many herbivorous waterbirds feed on seeds during moult, and moult migration is not necessarily north–south directed.

Post-glacial establishment of macrophyte populations could of course have occurred by exozoochory rather than endozoochory, but all of the above mentioned constraints for endozoochorous dispersal also apply for exozoochorous dispersal, with the exception of the ones associated with the functioning of the gut. In future studies these aspects should thus also be considered in detail by researchers interested in exozoochorous dispersal.

In addition to filling the gaps in knowledge identified by Figuerola and Green (2002), we feel that a fruitful approach would be to study a specific system in more detail. As a study system, we suggest a moult migration, where moulting birds feed on seeds and move between potentially suitable habitats. Moulting waterbirds are easily caught since they are flightless, enabling the attachment of satellite transmitters to the birds with which individual migratory itineraries can be mapped. The behaviour and morphology of the birds prior to departure should shed more light on the importance of fasting and gut atrophy. Attempts should also be made to obtain birds immediately before departure and upon arrival in order to determine the likelihood of seed transport. Alternatively, retention times of seeds could be measured while flying ducks in a wind-tunnel. Together with a quantification of the number of birds performing the journey, an estimate should be made of the probabilities of long-distance dispersal. This should then be combined with studies of the genetic make-up of the plant populations at the extremes of the moult migration route in order to determine the effective gene flow.

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Appendix 1.

The data compiled by Hedenström and Alerstam (1992) of the observed maximum fuel carrying capacity h_{max} ($= M_{max} / M_0$) gave the following allometric relationship: $h_{max} = 1.42\ M_0^{-0.0554}$ ($N = 41$, $r^2 = 0.66$), where M_0 is the lean and M_{max} is the maximum body mass (kg). For body mass M (kg) we took the average of minimum and maximum body mass of males and females according to Cramp and Simmons (1977), and regarded this as the body mass with 50% of the maximum reserves. We thus calculated M_0 as: $M_0 = M / (1 + 0.5\ (h_{max} - 1))$, equating h_{max} to the predicted h_{max} by iteration. The maximum fuel load F_{max} (kJ) a bird can carry then equals $e\ (h_{max} - 1)\ M_0$, where e is the energy density of fuel stores, taken as 30,000 kJ kg^{-1} (Klaassen, 1996).

We calculated the flight costs C (kJ km^{-1}; i.e., the work performed per unit distance) according to Pennycuick (1989) with a body drag coefficient of 0.1 (Pennycuick et al., 1996a). The wing span b (m) was taken from Cramp and Simmons (1977). We assumed flying at maximum range speed V_{mr} (the flight speed that enables the longest distance flown) for birds < 2 kg, and at the minimum power speed V_{mp} (i.e., the flight speed at which the rate of energy expenditure is minimal) for birds > 2 kg. For the smaller birds this overestimates the flight costs since the observed flight speeds were generally less than V_{mr} (see below), but this error is small due to the small change of the work per unit distance in the range between $(V_{\mathrm{mp}} + V_{\mathrm{mr}})/2$ and V_{mr} (Pennycuick, 1997). Alternatively, we calculated C from the allometric equation provided by Norberg (1996): $C = (51.5\ M^{1.37}\ b^{-1.60})/(V_{\mathrm{obs}}/3.6)$, where V_{obs} (km h^{-1}) are observed flight speeds corrected for wind effects and altitude. This allometric relationship is based on measurements of flight costs of birds ranging in body mass from 0.03 to 1 kg.

V_{obs} was taken from the literature, if available. For the species we did not have data; we used a predicted flight speed based on an allometric relationship derived from these and other literature data on waterfowl (Table 1). As predicted by aerodynamic theory, the observed flight speeds are an increasing function of body mass: $V_{\mathrm{obs}} = 63.0\ M^{0.075}$ ($r^2 = 0.16$, $N = 15$, one-sided $P < 0.05$). These speeds are between V_{mp} and V_{mr} for birds < 2 kg, and close to V_{mp} for larger birds (Fig. 6). This discrepancy between observed flight speeds and maximum range speeds, and a closer fit with minimum power speed with increasing body mass, has been noted before (Pennycuick, 1997; Bruderer and Boldt, 2001). Comparing data from Table 1 with the flight speeds of 139 European birds by Bruderer and Boldt (2001), among which only three species of waterfowl, shows that after correcting for body mass waterfowl species have much higher flight speeds than non-waterfowl species.

The maximum flight time is Tf_{max} (h) $= F_{\mathrm{max}} / (C\ V_{\mathrm{obs}})$. Retention time Tr (h) was calculated from the digestive tract length Lt (m), dropping length Ld (cm) and dropping interval (i.e., the time between subsequent droppings) Td (s) as given by Bruinzeel et al. (1997): $Tr = 0.0278\ Lt\ Td\ /\ Ld$. Data on Ld or Td were not available for all species, but these were closely correlated with body mass (using Bruinzeel's body mass data) ($Ld = 0.0453\ M^{0.456}$, $r^2 = 0.99$, $N = 7$ and

Table 1

Observed flight speeds V_{obs} in waterfowl. If more than one reference was available the average is presented. Body masses M after Cramp and Simmons (1977)

Species	M (kg)	V_{obs} (km h^{-1})	Reference
Garganey (*Anas querquedula*)	0.40	51.8	Bruderer and Boldt, 2001
Long-tailed duck (*Clangula hyemalis*)	0.72	50.4	Spiers, 1945
American wigeon (*Anas americana*)	0.74	63.7	Tucker and Schmidt-Koenig, 1971
Gadwall (*Anas strepera*)	0.77	74.5	Tucker and Schmidt-Koenig, 1971
Pintail (*Anas acuta*)	0.82	59.8	Tucker and Schmidt-Koenig, 1971
Mallard (*Anas platyrhynchos*)	1.09	78.5	Bruderer and Boldt, 2001; Belrose and Crompton, 1981
Black duck (*Anas rubripes*)	1.19	64.4	Tucker and Schmidt-Koenig, 1971
Brent goose (*Branta bernicla*)	1.44	65.3	Green and Alerstam, 2000
Barnacle goose (*Branta leucopsis*)	1.74	68.4	Rayner, 1985
White-fronted goose (*Anser albifrons*)	2.02	54.0	Rayner, 1985
Eider (*Somateria mollissima*)	2.15	75.6	Rayner, 1985
Snow goose (*Anser caerulescens*)	2.63	75.6	Belrose and Crompton, 1981
Canada goose (*Branta canadensis*)	4.43	63.7	Tucker and Schmidt-Koenig, 1971; Belrose and Crompton, 1981; Wege and Raveling, 1984
Bewick's swan (*Cygnus columbianus bewickii*)	6.05	68.4	Rayner, 1985; J.H. Beekman et al., unpublished
Whooper swan (*Cygnus cygnus*)	10.16	75.6	Pennycuick et al., 1996b

Table 2

Background data of 11 waterbird species used to calculate maximum flight distances and potential mean dispersal distances given in Fig. 5. P and N indicates calculations based on aerodynamical theory (Pennycuick, 1989; modified) and allometry (Norberg, 1996), respectively. Scientific names of all species are provided in the text and Table 1 except for the greylag goose (*Anser anser*)

Species	Body mass M (kg)	Wing span b (m)	Observed flight speed V_{obs} (km h^{-1})	Flight costs C (kJ km^{-1})		Max fuel carrying capacity h_{max}	Max reserve load F_{max} (10^3 kJ)	Max flight time Tf_{max} (h)		Digestive tract length Lt (m)	Dropping length Ld (cm)	Dropping interval Td (s)	Retention time Tr (h)
				P	N			P	N				
Teal	0.30	0.61	58[a]	1.1[c]	1.4	1.54	3.9	63	49	1.22	2.5	196	2.7
Wigeon	0.70	0.81	64[b]	2.4[c]	2.5	1.47	8.0	52	50	1.28	3.5	168	1.7
Pintail	0.82	0.88	60	2.7[c]	2.9	1.46	9.1	56	52	1.73	4.4	211[a]	2.3
Mallard	1.09	0.90	78	3.8[c]	3.2	1.43	11.6	38	47	1.43	4.6[a]	239[a]	2.1
Brent goose	1.44	1.15	65	4.4[c]	3.8	1.41	14.8	51	60	1.98	5.1[a]	243	2.6
Barnacle goose	1.74	1.39	68	4.7[c]	3.4	1.39	17.2	53	73	1.91	5.5	280	2.7
White-fronted goose	2.02	1.48	54	6.9[d]	4.8	1.38	19.5	52	75	1.73	6.2[a]	303[a]	2.3
Greylag goose	3.36	1.64	69[a]	12.2[d]	6.4	1.34	29.6	35	66	2.04	8.1	266	1.9
Bewick's swan	6.05	1.96	68	22.0[d]	10.9	1.30	47.1	31	63	2.77	10.1	523	4.0
Whooper swan	10.16	2.31	76	37.0[d]	15.4	1.26	70.3	25	60	3.17	11.8	451	3.4
Mute swan	10.75	2.23	75[a]	41.0[d]	17.7	1.26	73.3	24	55	4.03	13.3[a]	718	6.0

[a] Calculated from allometric relationship.

[b] American wigeon (*Anas americana*).

[c] at maximum range speed, V_{mr}

[d] at maximum power speed, V_{mp}

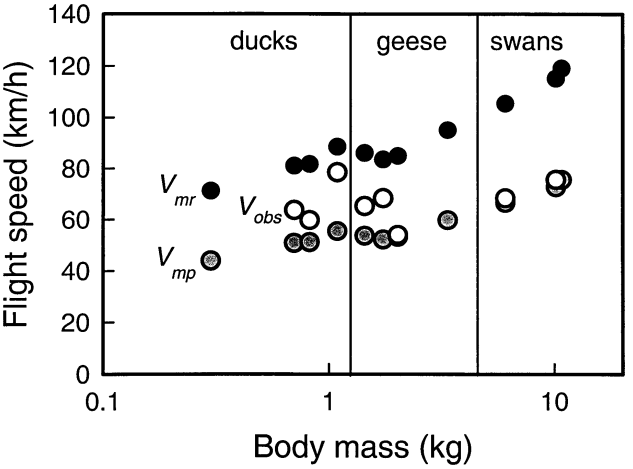

Fig. 6. Flight speeds of Anatidae versus body mass. For waterfowl < 2 kg observed speeds V_{obs} corrected for wind effects (white dots) were intermediate between the calculated maximum range speed V_{mr} (black dots) and minimum power speed V_{mp} (grey dots). For waterfowl > 2 kg, V_{obs} were close to V_{mp}.

$Td = 235\ M^{0.363}$, $r^2 = 0.84$, $N = 8$), and we used these allometric relationships to calculate Ld or Td in the missing cases.

The maximum flight distance is $Sf_{\max}$ (km) = $F_{\max} / C$. The potential mean dispersal distance is Sd (km) = $V_{\mathrm{obs}}\ Tr$. All variables included in the calculations are given in Table 2.

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