The effect of inter-specific differences in morphology and behaviour between dabbling duck species on the endozoochorous dispersal of aquatic organisms

Sanne Westbroek (3344711), supervised by Erik Kleyheeg and Merel Soons

Wetlands are highly threatened by human impact. About half of the world's wetlands were lost in the past century, resulting in larger distances between separate wetland areas. As a consequence, there is an increased isolation of these areas and a reduction in dispersal between them. In order to gain knowledge about the effects of wetland loss on the biodiversity of these areas, more information is needed about vectors regulating dispersal of organisms between wetlands. Because of their long-distance movements, diet composition, high abundance and widespread distribution in wetlands, dabbling ducks are considered important dispersal-vectors in these areas. During this study, the effects of inter-specific differences in morphology and behaviour between dabbling duck species on the endozoochorous dispersal of aquatic organisms was analyzed by means of a literature research. It was shown that different species of dabbling ducks are highly different in the resources they consume when there is a high amount of competition, or when the primary resource is scarce. Whether these inter-specific differences in diets result in differences in dispersal of aquatic organisms needs to be investigated. Furthermore it became clear that inter-specific differences between seeds are more important determinants of GRT than morphological differences between duck species. However, differences in movement patterns between dabbling duck species probably do influence different dispersal patterns of aquatic organisms. Different duck species exhibit a great variety of long-distance movements. Besides long-distance movements, short distance movements are also important for the dispersal of aquatic organisms. The global population size of a duck species determines the impact that varying duck species have on the dispersal of aquatic organisms. Even though species containing extremely large populations are probably more important for dispersal of aquatic organisms on a global scale, highly endangered duck species might be important for the dispersal of aquatic organisms on a local scale. Despite the fact that quite a lot is known about the dispersal of aquatic organisms by dabbling ducks, there are still many factors that need to be elucidated. More knowledge about differences in dispersal between varying dabbling duck species could not only lead to better measures to conserve wetlands, but also to stricter conservation measures to protect endangered dabbling duck species.

Introduction

Dispersal can be defined as "the movement of individuals away from their home-range" (Stenseth & Lidicker, 1992). The process of dispersal is highly important for the movement of genes between populations and the colonisation of new areas (Trakhtenbrot *et al.*, 2005). Especially the relatively rare long distance dispersal events can have large effects on local biodiversity and population structure. These events to a large extent determine the movement of individuals between populations, the spread of the population, and colonisation of species in new areas (Nathan *et al.*, 2008).

An ecosystem where long distance dispersal events are particularly important to maintain biodiversity are freshwater wetlands. Wetlands are areas where the environment and associated habitat are for most part controlled by water. They can be defined as "an ecosystem that arises when inundation by water produces soils dominated by anaerobic processes, which, in turn, forces the biota, particularly rooted plants, to adapt to flooding" (Keddy, 2010). Wetlands are highly threatened ecosystems. In the past century about half of the world's wetlands were lost due to human impact. There are many causes for this high amount of loss, for example drainage for agriculture,

development of infrastructure, control of malaria, forestation, building of dams etc. Furthermore ecological processes of wetlands are disrupted due to nitrification caused by industrial sources and agriculture (Silva *et al.*, 2007).
Wetlands are often highly isolated from other aquatic ecosystems and are therefore considered “islands in a sea of land” (Darwin, C. in Darwin, 1909). However, the biodiversity within wetlands is often relatively high (something that already astonished Darwin). This implies that, despite the geographic isolation of these areas, there is still sufficient dispersal of aquatic organisms between them (Darwin, 1859, via Van Leeuwen *et al.*, 2012 a). This indicates that wetland areas are ecologically linked. Because dispersal between different wetlands is such an important factor determining local diversity, the consequences of loss of these areas on local diversity might be disproportionally high. Loss of wetland area results in increased distances between wetlands and thereby in an even higher degree of isolation of the remaining areas. This causes major reductions in local dispersal. In order to determine how biodiversity of wetlands responds to human impact, more knowledge about the vectors that regulate dispersal of aquatic organisms between wetlands is needed (Soons, 2006; Santamaría & Klaassen, 2002; Wongriphuck *et al.*, 2008; Charalambidou & Santamaría, 2005).

Because of their high abundance, frequency of movements between ecologically similar habitats and their wide distribution, water birds are considered suitable dispersal vectors within and between wetlands (Green *et al.*, 2002; Figuerola and Green, 2002). Especially Anatidae (geese, swans and ducks) are important vectors because they often perform long distance movements. Furthermore, plant seeds as well as aquatic invertebrates are important components of the diets of many species of Anatidae (Green *et al.*, 2002). Several studies, both in the field and in the laboratory indicate that ingested propagules (e.g. plant-seeds and eggs from aquatic organisms) frequently survive passage through the duck guts, and that dabbling ducks have the potential to disperse aquatic organisms (Charalambidou *et al.*, 2003; Soons *et al.*, 2008; Raulings *et al.*, 2011; Figuerola *et al.*, 2010). There are two ways in which aquatic organisms can be dispersed by dabbling ducks. First of all they can be dispersed externally (epizoochory), by adhering to the bill, feet or feathers. Secondly, they can be dispersed internally (endozoochory) in the crop, followed by regurgitation, or through gut passage followed by defecation (Figuerola & Green, 2002; Charalambidou & Santamaría, 2002). Only the endozoochorous dispersal (gut passage followed by defecation) of aquatic organisms will be reviewed here, since only a very small amount of data is available on epizoochory (Van Leeuwen *et al.*, 2012 a). Furthermore, during a study on teal, Brochet *et al.* (2010a) found that endozoochory is much more important for the dispersal of aquatic organisms than epizoochory. In this study, we will focus on dispersal of aquatic organisms by dabbling ducks, the most studied and most abundant Anatidae on inland wetlands (Green *et al.*, 2002). We will analyse how variation between dabbling duck species from all over the world affect the dispersal patterns in wetland ecosystems.

Duck species have a number of properties that could result in inter-specific differences in dispersal of aquatic organisms. First of all, different dabbling duck species different diets. When dabbling duck species occur in the same habitat, they might forage in other parts of the vegetation and/or consume other aquatic species (Guillemain *et al.*, 2002; Gurd, 2007; Gurd, 2008; Green, 1998). Furthermore, variation in gut passage and gut passage rates between different species might influence seed viability and the transport distances of the aquatic organisms. For example, seed viability might be influenced by the weight of the gizzard. Figuerola *et al.* (2002) suggest that when species have a heavier gizzard, a larger part of the ingested aquatic organisms will be destroyed. However, when species with more grit in their gizzard ingest seeds, the seeds will germinate better (Figuerola *et al.*, 2002). Besides the gizzard size and amount of grit in the gizzard, viability could be influenced by dissimilarities in chemical and physical digestion in the guts (Charalambidou *et al.*, 2003; Brochet et al., 2010b). Finally, dispersal distances are influenced by the varying migration strategies of different species. Variations in migratory movements, distances and frequencies will result in different dispersal patterns (Viana *et al.*, 2013).

During this study, the effects of inter-specific differences in morphology and behaviour between dabbling duck species on the endozoochorous dispersal of aquatic organisms will be analyzed. This will be done by means of literature research. First of all, the different diets of dabbling duck species will be studied by assessing the deviations in foraging behaviours and morphological features of the different species. Subsequently gut passage rates and migration strategies will be examined to see where the aquatic organisms will end up. Finally, population sizes of duck species will be investigated to assess the likeliness of dispersal of aquatic organisms by these vector species.

Different dabbling duck species, different diets

In order to understand how it is possible that morphologically highly similar species can have very differentiated diets, first we will explain why different species of dabbling ducks consume different resources. We will then describe how their feeding mechanism works. Finally, these results will be presented in a table for all species of dabbling ducks.

Resource partitioning

Even though dabbling duck species are highly similar to each other, different species of dabbling ducks consume different resources. This is called resource partitioning. The resource which is most beneficial for a species is called the primary resource. There are two kinds of resource partitioning. In the first type of resource partitioning, species with different primary resources benefit most from the availability of these different resources. In this case, there is no competition between the different species (Rosenzweig, 1981 via Gurd, 2007).

In the second type of resource partitioning, different species have a preference for the same resource. In this case, the different species benefit most when they can exploit the same resource (primary resource), however when this resource becomes scarce, they have distinct preferences for the secondary resource (which is less profitable). These species will share the same diet when competitors are scarce or when the primary resource is abundant (Rosenzweig & Abramsky, 1986 via Gurd, 2007).

Models developed by Gurd (2008), based on bill morphology and kinetics of seven species of dabbling ducks, predict that these species prefer the same prey. So, when prey is abundant and competition is low, these duck species should forage on the same resources, when competition is high, and the amount of prey is low, they will partition their resources and forage on the secondary resource (Gurd, 2008). This was also shown in a study from Nummi & Väänänen (2001) and Guillemain (2002).

Which secondary resources are foraged on by dabbling ducks is linked to the morphological features of the species; these include bill shape and body size. In the next paragraphs these characteristics will be discussed further.

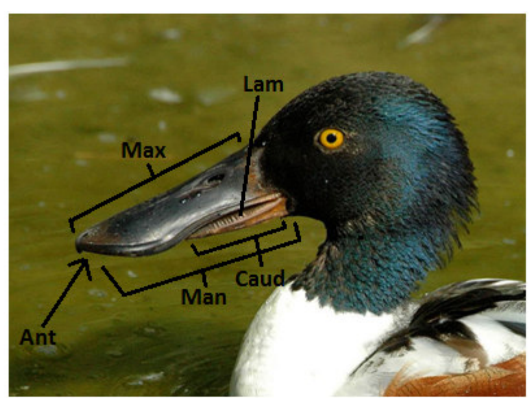


Figure 1. Picture of the head of a northern shoveler, sowing the anterior side of the bill (Ant), where water enters when the duck opens its bill, the maxilla (Max), mandible (Man), the caudal end, where the water is expelled during filter feeding (Caud) and the lamellae (Lam). Picture adapted from http://npc9.wordpress.com.

Feeding mechanisms of dabbling ducks

Dabbling ducks feed primarily by means of filter feeding. They open their bill and retract the elevated lingual bulges. This causes a flow of water and prey to enter the oral cavity through the anterior opening between the maxilla and mandible. After this, the bill closes and the lingual bulges protract, squeezing the water out of the caudal end of the bill cavity. The water and prey flows along lamellae at lateral edges of the

mandible and maxilla. Here the prey is either retained by the lamellae, or excreted with the flow of water (Figure 1) (Kooloos & Zweers, 1991; Gurd, 2007).
Particles are sieved out of the water flow when they are larger than the distance between the lamellae, or when they are larger than the space between the mandible and maxilla (Gurd, 2006). Though many particles are retained by means of sieving, some particles are retained when they pass through the filter lamellae because of their mass. This is called inertial impaction. When the water containing the particle comes near the lamellae, the streamline of the water will accelerate and divert. Because of the mass of the particle, the particle will slow down and deviate from the streamline. When the distance between the particle and the lamellae is within one particle radius, it will be intercepted (Rubenstein & Koehl, 1977).
Besides inertial impaction and filter-feeding, ducks also have other feeding mechanisms. First of all, they can peck food. In order to transport the food trough the bill, they use a "catch and throw mechanism". Furthermore, dabbling duck species can graze; hereby they pull up vegetative parts of plants. Finally, some duck species put their bill in the mud and then grasp for food. The proportions in which these feeding mechanism are used vary per duck species. Some are more specialised in grazing, while others are more specialised in filter feeding (Kooloos & Zweers, 1991).

Bill shape and diets

Even though there are similarities between the bills of different species of dabbling ducks, e.g. they are all flat and lined with lamellae internally (Brochet *et al.*, 2012), there are also many varieties of bill shapes. They come in many shapes and sizes; some are very large and spoon shaped (e.g. shovelers) while others are very small and shaped like a little finger (common teal, *A. crecca*). These different shapes are an adaptation to the different resources these species consume. Many dabbling duck species are capable of consuming a relatively broad range of foods. However, there are some that are more specialised. Hereunder the most common bill shapes and associated diets will be discussed. Even though differences in bill shape are often associated with different diets, these two are not always linked. Since scientific information about the correlation between bill shape and diet is limited, the information is mainly from the website www.ducks.org, written by biologist Davis, B. All dabbling duck species will be divided in four groups based on their bill shapes in Table 2. These groups are: Omnivores, grazers, granivores, and carnivores.

Omnivores

A bill shape that is typical for species with an omnivorous diet is that of the mallard (Table 1). Omnivorous duck species have a broad range of food sources. They consume nearly anything they can find. For example, vegetative parts and seeds of aquatic plants and crops, and in spring and summer they also consume aquatic and terrestrial invertebrates like molluscs, crustaceans, worms, insects and sometimes even amphibians and fish (del Hoyo *et al.*, 1992). In Table 2 it is shown that an omnivorous bill shape is linked to an omnivorous diet in 17 out of 18 duck species. An exception is the Auckland teal, which is mainly a carnivorous species.

Grazers

The bills of grazing dabbling duck species are generally narrower and stubbier than the bill of the mallard, making it especially easy to tear off the tops of green shoots (Table 1) (Davis, www.ducks.org). Grazing species often forage in pastures, and consume grasses, sedges, and greener parts of crops and aquatic plants (del Hoyo *et al.*, 1992). In Table 2 it is shown that the grazer bill shape is linked to a grazing diet in 3 duck species ((Eurasian wigeon, *A. penelope*; American wigeon, *A. americana*; Chiloe wigeon, *A. sibilatrix*).

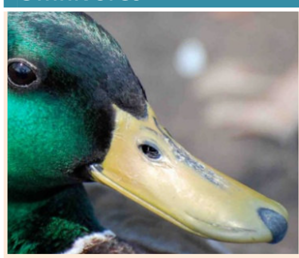
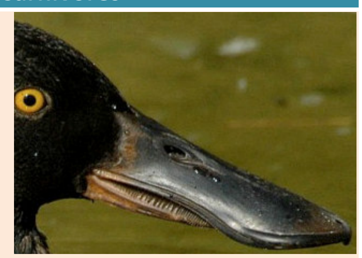
Granivores

Bill shapes of seed eating dabbling duck species are generally similar to the mallard's bill, only smaller. An exception is that of the common teal, this specie's bill is shaped like a small little finger, having the same width across the whole length (Table 1). Species with these bill shapes mainly consume seeds, vegetative parts of aquatic vegetation, grasses and sedges, and sometimes small aquatic invertebrates (del Hoyo *et al.*, 1992). Table 2 shows that 7 species of dabbling ducks have bill shapes adapted to consumption of seeds. Diets of all these species for a large part consist of seeds (del Hoyo *et al.*, 1992).

Carnivores

Carnivorous bill shapes are generally spoon-shaped, flattened, and very wide with distinct lamellae. This extraordinary bill helps them filter invertebrates (e.a. crustaceans) from the water surface (Table 1). Carnivorous duck species often do eat plant matter in winter, when aquatic invertebrates are scarce. Their diet mainly consists of insects (and their larvae), molluscs, crustaceans, some amphibians, seeds and vegetative parts of aquatic plants (del Hoyo *et al.*, 1992). Table 2 shows that there are 4 dabbling duck species with a carnivorous bill shape. 3 of these species mainly consume invertebrates. There is however one exception, the red shoveler (*A. platalea*) is mainly a vegetarian (del Hoyo *et al.*, 1992)

Table 1. Bill shapes associated with different diets. From left to right; American wigeon (*A. Americana*); Common teal (*A. crecca*); mallard (*A. platyrhynchos*); northern shoveler (*A. clypeata*). Pictures adapted from www.petchary.wordpress.com, www.commons.wikimedia.org, http://www.urbanwildlifeguide.net, http://seanetters.wordpress.com

Omnivores	Grazers	Granivores	Carnivores
			

Lamellar densities

Besides the shape of the bill, some internal features of the bill are also important determinants of food segregation among dabbling ducks. There are many studies that have shown that ducks with larger inter-lamellar distances (Figure 2) also consume larger particles. Due to differences in density of the lamellae, different duck species are able to consume different prey sizes. However, the importance of lamellar density for the selection of particles is different for different species of dabbling ducks (Textbox 1).

Nudds & Bowlby (1984) already showed that the distributions of prey sizes are different in different species. Furthermore, they found a negative correlation between the density of lamellae and prey size. During another study by *Nudds et al.* (1994) it was shown that species with high lamellar densities foraged more in offshore, open habitats, while species with lower lamellar densities foraged more in inshore, vegetated habitats. This was probably because offshore open habitats contain more fine prey species than inshore vegetated habitats.
However, there are also some studies that did not find a correlation between lamellar densities and prey size. For example Nummi & Väänänen (2001) found a high level of diet overlap between six species of dabbling ducks. This was probably due to a high amount of resources, which results in a lack of competition. Furthermore, this study only focuses on a small part of the bird's life-cycle, and it was conducted in summer, when there is less competition. In order to get more complete information about diet segregation, feeding patterns will also have to be studied in winter. Thomas (1982) via Brochet *et al.* (2012) also could not find any difference in sizes of ingested propagules between mallard, common teal, northern shoveler, Eurasian wigeon and garganey (*A. querquedula*). This was probably also due to a lack of competition.

A study by Guillemain *et al.* (2002) which started in September and ended at the end of the winter showed that there was a high amount of diet overlap between mallard and teal during the start of winter, but later in the season, when resources became scarce, the species partitioned their resources (Guillemain *et al.*, 2002).

During another large-scale study by Brochet *et al.* (2012), a large amount of data from 59 studies about diets of mallard, pintail and teal was used. They indeed showed that different species ingest different seed sizes, and that these seed sizes are dependent on lamellar densities. The longest, heaviest and widest seeds were consumed by the mallard, which was the largest investigated species with the largest spacing between its lamellae. The smallest seeds were consumed by the smallest species with the least space between its lamellae. This indicates a negative correlation between seed size and lamellar density.

From the above studies it can be concluded that diet segregation between different dabbling duck species is dependent on the amount of resources that is available. When a high amount of resources is available, dabbling ducks will use the foraging method and resource that is most beneficial, which is often an overlapping resource. However, when this resource becomes scarce they will forage on a secondary resource, which is determined at least partly by lamellar density. In Table 2 the different lamellar densities of varying dabbling duck species are shown.

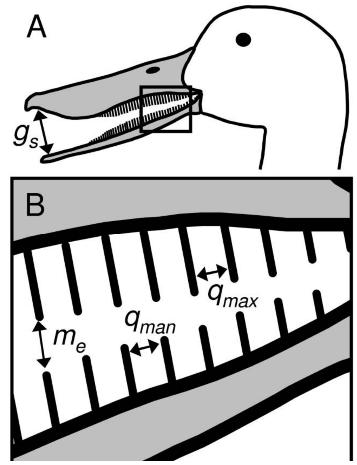


Figure 2. A: Schematic profile of the head of a northern shoveler, showing the gape (gs), where prey and water enters the oral cavity. The lamellar filter, where particles are retained is surrounded by a rectangle. **B**: Schematic closu-up of the lamellae. m_e: Lamellar separation, which is the distance between the top of the mandibular lamellae and the top of the maxillary lamellae. q_{man}: Inter-lamellar distance between the lamellae on the mandible. q_{max}: Inter-lamellar distance between th lamellae on the maxilla. Picture cited from Gurd, 2007.

Textbox 1: Different duck species, different ways to select particles

The way ducks select particles might be different for different duck species. It is found that increasing the space between the mandibular or maxillary lamellae reduces the number of particles ingested by the northern shoveler (*Anas clypeata*). However, the number of particles ingested by mallards (*A. platyrhynchos*) was not reduced. This indicates that shovelers (small distance between lamellae) primarily select their prey by sieving, while mallards (larger distance between lamellae) select prey items that are smaller than the distance between lamellae by inertial impaction, and larger prey items by sieving (Kooloos *et al.*, 1989).

Active selection of particles by size

Even though many studies find a relationship between the inter-lamellar distance and minimum size of ingested prey, a study by Gurd (2006) states that the inter-lamellar distance is not always the only factor determining which particles will be ingested. He showed that dabbling ducks are able to actively select particles by size.

During Gurds study, millet, wheat and poppy seeds were fed to three ducks (one northern shoveler and two mallards). All three seed types were larger than the distance between the lamellae. The ducks ingested less of the less preferred poppy seeds, and more of the preferred millet- and wheat seeds, indicating that they probably actively expelled the poppy seeds.

Gurd showed that ducks can actively change their lamellar spacing by elevating and depressing the mandible and maxilla. This changes the distance between the maxillary and mandibular lamellae. As a result, ducks are able to expel particles that are larger than the distance between adjacent lamellae (Gurd, 2006).

Although the study from Gurd (2006) was based on just three individuals, all three individuals showed consistent results. However, in order to state that all individuals and species of dabbling ducks can actively expel particles that are larger than the distance between adjacent lamellae, more species and individuals need to be investigated. The finding of this mechanism complicates the negative correlation between lamellar density and prey size, but it does not exclude this correlation.

A small distance between adjacent lamellae allows ducks to sieve both small and large particles at a relatively low energy cost. But if this is the case, what is the advantage of a larger distance between the lamellae? Tolkamp (1993) suggests that more space between the lamellae might reduce blockage of the lamellae by detritus, blockage reduces the water flow through the bill. However, the larger spacing results in a lower amount of ingestion of small prey items. Different lamellar densities are probably trade-offs that are needed for partitioning of resources between species (Tolkamp, 1993 via Gurd, 2006).

Body Length

Besides bill shape and lamellar densities, different diets are also correlated with different body lengths of varying dabbling duck species. Dabbling duck species are able to dive, but they rarely do it. In order to reach prey particles that are at the bottom (or deeper in the water), they will up-end. This means that they put their head and neck down in the water and their rear end towards the sky. In this way, only the front half of their body is submerged (Figure 3). How deep a duck species can reach depends on the body length of the species. When different species have different body lengths, they will segregate along different foraging depths (Guillemain *et al.*, 2002; Pöysä, 1983). For example, during a study on the influences of morphology on organisation of niches among six species of dabbling ducks, Pöysä (1983) showed that differences in body and neck length allowed ducks to use the feeding habitat in different ways. The body lengths of different species of dabbling ducks are shown in Table 2.

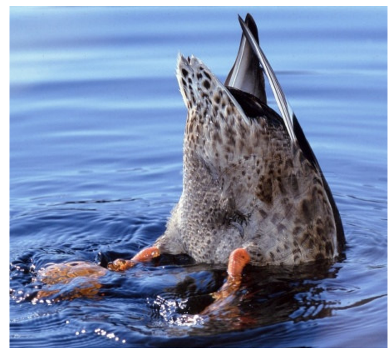


Figure 3. Up-ending mallard. Picture adapted from: www.warrenphotographic.co.uk

Whether segregation between different dabbling duck species depends on body length is determined by the shape of the water basin. Basins can be roughly divided in two shapes; shallow, gently sloping basins and deep, steep basins (Figure 4). In the first type, almost all duck species can reach the bottom in most parts of the pond. Therefore, there is a horizontal segregation between species depending on prey size, which is determined by the lamellar densities. Prey size is different in different parts of the pond. It is usually larger along the more vegetated edges of the pond and smaller in centre parts of the pond. This results in duck species with diets consisting of larger particles to forage along the edges of the pond, while duck species foraging on smaller particles go to the centre of the pond (Nudds *et al.*, 2000).

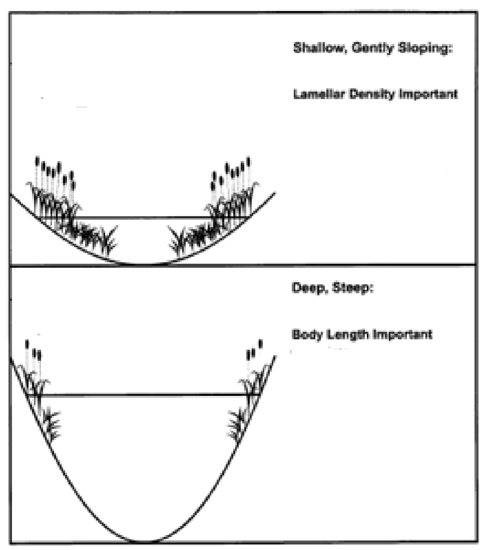


Figure 4. Above: Illustration of a gently, shallow sloping basin, where food segregation is dependent on lamellar densities. Below: Deep, steep basin, where food segregation is dependent on body length. Figure adapted from: Nudds *et al.*, 2000.

In the deep and steep basins, in the centre of the pond, the bottom is unreachable for all species of dabbling ducks. Therefore, they are all restricted to the edges of the pond. This results in the segregation of species that is dependent on the foraging depth, which is determined by body length (Nudds *et al.*, 2000).

The role of lamellar density combined with body length

Guillemain *et al.* (2002) studied the influence of both the lamellar density and body length of mallard and common teal on different diets of these species. During that study it was shown that mallard and teal foraged on the same prey size and depth during the start of the winter. They both fed in shallow water on larger seeds, because this is most profitable in terms of energy cost. However, later in winter when the most profitable food (primary resource) became scarce, the two species segregated. The mallard, which is the largest of the two species, started foraging at greater depths. Teal, which has the highest density of lamellae, started consuming smaller particles. So, both lamellar density and body length allowed segregation of resources between these species, and thereby resulted in different diets when the primary resources became scarce (Guillemain *et al.*, 2002).

In Table 2 the different lamellar densities and body lengths of varying dabbling duck species are shown.

Gut Retention Times

In order for aquatic organisms to be endozoochorously dispersed by dabbling ducks, they have to pass through the digestive system. So, beside the different diets of varying duck species, differences in dispersal of aquatic organisms are also determined by differences in passage through the digestive tract. Whether and where ingested propagules germinate is dependent on differences in the digestive tract between duck species, the size and weight of the seeds, and the retention time (from ingestion to excretion) (Charalambidou *et al.*, 2003).

Gut Retention Times (GRT)

An important factor determining where ingested particles will end up during bird movement, is the gut retention time (GRT). The gut retention time is the time it takes for an ingested propagule to be excreted. Besides the dispersal distance, gut retention time also influences viability of the propagules; a longer retention time results in greater damage and thereby lower viability of ingested seeds (van Leeuwen *et al.*, 2012 a). This was confirmed during a study by Charalambidou *et al.* (2003). During that study it was shown that seeds that were excreted earlier were more likely to germinate, and therefore had a higher chance of successful dispersal. Furthermore, Charalambidou *et al.* multiplied the average flight speed of five duck species (Eurasian wigeon, mallard, common teal, northern shoveler and northern pintail; A. *acuta*) with retention times to calculate the average dispersal distances. They estimated that with average flight speeds ranging from 10 to 70 km h^{-1}, average dispersal distances were between 40 and 280 km. Soons *et al.* (2008) also multiplied GRT values with flight speeds of mallards, however instead of the average dispersal distances, they calculated maximum dispersal distances. Soons *et al.*

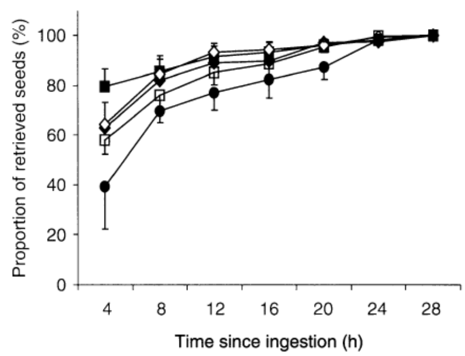


Figure 5: Percentage of ingested *Ruppia maritima* seeds retrieved over time by five species of dabbling ducks. Teal, filled circle; Wigeon, empty rhombus; Shoveler, empty square; Pintail, filled square; Mallard, filled rhombus. Image cited from Charalambidou *et al.*, 2003

found a maximum dispersal distance of 780 km for most seeds and up to 3000 km for the smallest seeds.

During the study by Charalambidou *et al.* (2003), retention time, germination and retrieval of seeds of wigeongrass after they passed through the digestive tract of the five *Anas* species were also investigated. Retention times were highly similar between different species of dabbling ducks (Figure 5). They showed that there were no differences in excretion and germination of seeds between the different duck species. It was suggested that differences in physiology and chemistry of the digestive tract between different duck species is not necessarily of importance when it comes to germination of the seeds and retention times. Miller already suggested this in 1984 when he found that there were no differences in the ability to obtain energy from foods between northern shoveler, northern pintail and gadwall (*A. strepera*). He concluded that physiology of the guts could be highly similar for different species of dabbling ducks (Miller, 1984).

Influence of particle properties on GRT

Size of the particles might be an important adaptive trait for the ingested organisms to be dispersed. In their meta-analysis, van Leeuwen *et al.* (2012 a) showed that smaller particles are retrieved more often than larger particles. They also showed that a particle of 10 mm is two times less likely to be endozoochorously dispersed than a particle of 1 mm. However, further research is needed to confirm this, since the statistical power for this finding was relatively low. During a study from Soons *et al.* (2008) 23 plant species that are common in wetland habitats were fed to mallards. They showed that the species with smallest seeds had the highest germination percentage after gut passage. It still has to be investigated whether smaller particles are more resistant to digestion, or whether it is easier for them to escape ingestion (van Leeuwen *et al.*, 2012 a). Besides the conclusion that smaller particles have the highest survival, small particles are also more abundant in nature, and therefore they are ingested more often than larger particles (Brochet *et al.*, 2010a).

Indigestible markers of different sizes were used to determine differences in retention time between smaller and larger propagules. It was shown that smaller markers had shorter retention times than larger markers (Van Leeuwen *et al.*, 2012 b). This indicates that larger propagules have the potential to be dispersed over greater distances.

Soons *et al.* showed that seed coat thickness is not so important for intact gut passage, but for some species it does determine whether gut passage results in successful germination or not. For example in species that are adapted to endozoochorous dispersal like the branched bur-reed (*Sparganium erectum*). This species germinates better after gut passage than in control situations. In this case, gut passage probably breaks or removes the seed coat (Soons *et al.*, 2008).

Different duck species, different movement patterns

Different movements of ducks determine where consumed aquatic organisms will end up. Here a distinction will be made between long distance movements and short distance, or local movements. Long distance movements are the migration movements during spring and autumn, when several duck species travel large distances between their wintering and breeding grounds. Short distance movements are the local movements made by sedentary species or by migratory species when they are at their nesting or wintering grounds.

Long distance movement

The maximum distance over which propagules might be endozoochorously dispersed, and where they will end up, is to a large extent determined by the different migration strategies of the different dabbling duck species.

As shown in Table 2, different dabbling duck species occupy varying migration strategies. Some species are unable to fly (e.g. Auckland teal, *A. aucklandica*), indicating that they can only disperse aquatic organisms on a local scale, while other species are highly migratory (e.g. garganey and northern pintail), flying distances of thousands of kilometres. This greatly increases the distances over which they can disperse aquatic organisms. Sometimes migration patterns do not only vary between species, but also within species. This is for example the case with mallards. Within this species, populations from northern regions migrate to more temperate regions before winter, while populations from more temperate and tropical regions are sedentary (del Hoyo *et al.*, 1992).

Whether or not birds migrate is to a large extend dependent on the latitude they come from. A larger proportion of bird species from higher latitudes migrate during winter than bird species from lower latitudes. A study by Newton and Dale (1996a) in eastern North America shows that the number of migrating bird species increases from 12% at 25˚N to 87% at 80˚N. They also show that the number of species that spend the winter in the south and migrate to the north after the winter decreases from 52% at 25˚N to none at 70˚N. The same patterns were found during another study in Western Europe (Newton & Dale, 1996b). However, these large movements are not without risk. The number of ducks moving to the south during autumn is much higher than the number of ducks returning in spring. This results in more southwards dispersal of aquatic organisms than northwards (Green *et al.*, 2002).

For the dispersal of seeds it is not only important how far the ducks travel, but also how many stop-over decisions they make. In a study by Lurz *et al.* (2002) a distinction was made between 'hoppers' and 'jumpers'. The 'hoppers' use a migration strategy where the lowest amount of energy is used. They go from one suitable stopover site to the other. Contrary to hoppers, 'jumpers' complete their journey as fast as possible. They will fly as far as possible before they stop, while 'hoppers' travel about one day each time and then search the landscape for a suitable stopover site (Lurz *et al.*, 2002). Whether duck species occupy the hopper or jumper strategy might have important influences on the gene flow of the dispersed aquatic organisms. It is expected that the strategy occupied by hoppers will result in higher gene flow over shorter distances, since these ducks stop in many suitable habitats. Furthermore, it is expected that larger duck species might be more important for the long-distance dispersal of seeds. Larger ducks are able to fly over larger distances before they make a stop-over decision (Lurz *et al.,* 2002).

There are several other characteristics that influence the distances different dabbling ducks can travel. These characteristics do not necessarily vary per duck species, but may also vary per individual duck (e.g. amount of accumulated fat, rate of fat and muscle burn (Gauthier *et al.*, 1992 via Lurz *et al.*, 2002; Pennycuick, 1998)). Furthermore, within species there might be differences in migration patterns between sexes and different age groups. Male and female ducks travel different distances during migrations in autumn and spring and during movements in winter (Lurz *et al.*, 2002).

Short distance movement

Despite the fact that not all duck species make long-distance movements, all duck species do make local movements, including movements between foraging areas and resting or nesting areas. These movements could result in dispersal of aquatic organisms between adjacent wetland areas. This type of dispersal can be especially important for organisms that are unable to disperse via other vectors (e.g. wind or water). Even when migratory birds are in their wintering grounds, they may still show many local movements. This is especially the case in more northern migratory birds. In response to cold weather, these birds often move between different wetlands (Pradel *et al.*, 1997). In other areas, for example in semi-arid and Mediterranean regions, birds often show large local movements in response to high amounts of rainfall (Green *et al.*, 2002).

Population sizes

The impact certain duck species have on the dispersal of aquatic organisms is dependent on the number of individuals there are.

The population sizes of various dabbling duck species are shown in Table 2. This table shows that there is a high variety of population sizes between different species of dabbling ducks. Some species are endangered and contain just a few thousand individuals (e.g. Auckland teal & meller's duck; *A. melleri*), while populations of other species are extremely large, containing millions of individuals (e.g. mallard, Eurasian wigeon & northern pintail). Populations containing only a few thousand individuals probably have a smaller impact on the dispersal of aquatic organisms than populations containing millions of individuals. However, species with small population sizes often occupy only a small range (Birdlife International; del Hoyo *et al.*, 1992), therefore they might be highly important for the dispersal of aquatic organisms on a local scale.

Table 2. Table with traits from dabbling duck species. S: Bill shape adapted to seed eating diet. O: Bill shape adapted to an omnivorous diet. C: Bill shape adapted to carnivorous diet. G: Bill shape adapted to grazing diet. Body lengths, weights, migratory strategies, diets, distribution from del Hoyo *et al.*, 1992. Population sizes from Birdlife International and references therein.

Taxonomic group	Species	Scientific name	Body-length (cm)	Weight (g)	Lamellar density (no./cm)	Migratory strategy	Diet	Bill shape	Global pop size	Distribution	Geographical zone
Baikal teal	Baikal Teal	*Anas formosa*	39-43	360-520		Migratory	Granivorous	S	Very large >1,060,000	E Siberia to Kamchatka	Polar, Temperate
Silver teals	Garganey	*Anas querquedula*	37-41	290-480		Highly migratory	Omnivorous	O	Extremely large: 2,600,000-2,800,000	Between 42°N and 65°N in the Palearctic	Polar, Temperate
	Silver Teal	*Anas versicolor*	38-43	442-373		Partially migratory	Omnivorous	O	Very large	South America, in Chile and Argentina	Temperate, Tropical
	Hottentot Teal	*Anas hottentota*	30-36	216-282		Mostly sedentary	Omnivorous	O	Very large	Madagascar, Ethiopia to Cape Provence	Temperate, Tropical
Blue-winged ducks	Blue-winged Teal	*Anas discors*	35-41	266-410	12.2 (Nudds & Bowlby, 1984)	Migratory	Omnivorous	O	Extremely large	USA, Canada and N of South America	Polar, Temperate
	Cinnamon Teal	*Anas cyanoptera*	35-48	400		Partially migratory	Omnivorous	O	Very large	W South America, W North America	Temperate, Tropical
	Red Shoveler	*Anas platalea*	45-56	523-608		Partially migratory	Granivorous	C	Moderately small to large	South America, most of Argentina, Tierra del Fuego to Chile,	Temperate, Tropical
	Cape Shoveler	*Anas smithii*	51-53	584-830		Mostly sedentary	Largely carnivorous	C	Moderately small to large	Namibia, Botswana, South Africa	Temperate, Tropical
	Australasian Shoveler	*Anas rhynchotis*	46-56	545-852		Mainly sedentary	Omnivorous	C	Moderately small to large	New Zealand, Tasmania, SW and SE Australia	Temperate
	Northern Shoveler	*Anas clypeata*	43-56	410-1100	21.5 (Hill et al., 2010)	Highly migratory	Largely carnivorous	C	Extremely large (5,500,000-6,000,000)	Most of Palearctic and Nearctic, except high Arctic	Polar, Temperate, Tropical
Wigeons	Eurasian Wigeon	*Anas Penelope*	45-51	415-970		Migratory	Grazer	G	Extremely large (2,800,000-3,300,000)	Iseland, N Asia, N Europe	Temperate and Polar
	American Wigeon	*Anas Americana*	45-56	680-770	11.0 (Hill et al., 2010)	Migratory	Grazer	G	Extremely large	NW to CE North America to NE California and N Colorado	Temperate and Tropical
	Chiloe Wigeon	*Anas sibilatrix*	43-54	828-939		Partially migratory	Grazer	G	Very large	Falkland Is., S of C Argentina, South America, C Chile,	Temperate
	Gadwall	*Anas strepera*	46-58	850-990	12.2 (Hill et al., 2010)	Partially migratory	Granivorous	S	Extremely large (3,200,000-3,800,000)	Palearctic and Nearctic	Temperate and Tropical
	Falcated Duck	*Anas falcate*	46-54	422-770		Migratory	Granivorous	S	Near threatened (>89,000)	N Japan, SE Siberia, Mongolia to Kuril Is.	Polar and Temperate
Pintails	Northern Pintail	*Anas acuta*	50-65	850	10.1 (Hill et al., 2010)	Highly migratory	Omnivorous	O	Extremely large (5,345,000-5,460,000)	Most of Nearctic and Palearctic	Temperate, Tropical, Polar
	Yellow-billed Pintail	*Anas georgica*	43-55	460-660		Partially migratory	Omnivorous	O	Very large	South America	Temperate, Tropical
	White-cheeked Pintail	*Anas bahamensis*	38-51	474-533		Mostly sedentary	Presumably granivorous	S	Very large	West indies, South America, Galapagos Is.	Tropical
	Red-billed duck	*Anas erythrorhyncha*	43-48	345-954		Mostly sedentary	Omnivorous	O	Very large	S Sudan, and S Ethipia to Cape Province and Angola, Madagascar	Temperate, Tropical

	Cape Teal	*Anas capensis*	**44-48**	**316-502**		**Mainly sedentary**	**Omnivorous**	**O**	**Very large**	**Sudan, Ethiopia to Namibia, South Africa**	**Temperate and Tropical**
Grey teals	**Madagascar Teal**	*Anas bernieri*	**40**			**Presumably sedentary**	**Unknown**	**O**	**Endangered (1,500-2,500)**	**W coastal Madagascar**	**Tropical**
	Sunda Teal	*Anas gibberifrons*	**37-47**	**395-670**		**Mostly sedentary**	**Granivorous**	**S**	**Moderately small to large**	**Andaman Is., New Zealand, Australia, Indonesia**	**Tropical, Temperate**
	Chestnut Teal	*Anas castanea*	**35-46**	**600-700**		**Mostly sedentary**	**Granivorous**	**S**	**Very large**	**SW and SE Australia, Tasmania**	**Temperate**
Green-winged teals	**Common Teal**	*Anas crecca*	**34-43**	**340-360**	**15.0 (Brochet et al., 2012)**	**Partially migratory**	**Granivorous**	**S**	**Extremely large**	**N and C Palearctic, Nearctic, Aleutian Is.,**	**Northern and Temperate**
	Yellow-billed Teal	*Anas flavirostris*	**35-45**	**600-830**		**Partially migratory**	**Omnivorous**	**S**	**Very large**	**South America**	**Tropical and Temperate**
Brown teals	**Auckland Teal**	*Anas aucklandica*	**36-48**	**375-700**		**Presumably sedentary, flightless**	**Carnivorous**	**O**	**Vulnerable (700-3500 mat.)**	**S New Zealand, Auckland Is.**	**Temperate**
	African Black Duck	*Anas sparsa*	**48-58**	**952-1077**		**Mainly sedentary movements**	**Omnivorous**	**O**	**Moderately small to large**	**W equatorial Africa, S Africa, S of Zimbabwe**	**Tropical**
Mallards	**Meller's Duck**	*Anas melleri*	**63-68**			**Presumably sedentary**	**Omnivorous**	**O**	**Endangered (2,000-5,000)**	**E and High Plateau Madagascar**	**Tropical**
	Yellow-billed Duck	*Anas undulata*	**51-58**	**630-1208**		**Mostly sedentary**	**Omnivorous**	**O**	**Very large**	**Uganda, Ethiopia, Kenya to Angola and Cape Provence, S Sudan**	**Tropical, Temperate**
	American Black Duck	*Anas rubripes*	**53-61**	**1150-1350**		**Partially migratory**	**Omnivorous**	**O**	**Very large**	**E Canada, S (North Carolina) to E USA**	**Temperate**
	Philippine Duck	*Anas luzonica*	**48-58**	**725-977**		**Mostly sedentary**	**Omnivorous**	**O**	**Vulnerable (5,000-10,000)**	**Mindoro , Luzon, Mindanao Is., Masbate**	**Tropical**
	Pacific Black Duck	*Anas superciliosa*	**47-61**	**700-1340**		**Mostly sedentary**	**Omnivorous**	**O**	**Very large (180,000-1200,000)**	**SW Pacific, New Guinea, Australia, New Zealand**	**Tropical, Temperate**
	Mallard	*Anas platyrhynchos*	**50-65**	**750-1575**	**8.0 (Hill et al., 2010)**	**Partially migratory**	**Omnivorous**	**O**	**Extremely large (>19,002,700)**	**Most of Palearctic and Nearctic**	**Polar, Temperate, Tropical**
	Spot-billed Duck	*Anas poecilorhyncha*	**58-63**	**750-1500**		**Partially migratory**	**Granivorous**	**S**	**Very large**	**Burma, Laos, S China, Assam, Troughout Indian subcontinent**	**Tropical, Temperate**

Discussion

From this study we can conclude that despite the high similarities between different species of dabbling ducks, they also contain a high variety of morphological features and behaviours. However for many of these features it is still uncertain how and whether they result in inter-specific differences in dispersal of aquatic organisms.

During this study it was shown that different species of dabbling ducks are able to consume different resources. When the resource is abundant and there are not many competitors, different species of dabbling ducks will share the same resource. However, when the resource becomes scarce, or when there is a high amount of competition, the different species will start foraging on different resources, resulting in inter-specific different diets (Rosenzweig & Abramsky, 1986 via Gurd, 2007).
Although it seems logical that different diets will lead to excretion of different organisms (and thereby to dispersal of different aquatic organisms), this is not necessarily the case. In spite of the different diets consumed by different species of dabbling ducks (Table 2), van Leeuwen *et al.* (2012a) found that species defined as omnivorous and herbivorous both excrete plant seeds and invertebrates. However, maybe the proportions in which they do this are different (e.g. species with herbivorous diets probably disperse more plant species than species with carnivorous diets). It is possible that species classified as herbivorous do forage on animal matter during the breeding season. Animal matter can also be ingested accidentally because it floats between plant material (van Leeuwen *et al.,* 2012a). Further research on comparisons between largely carnivorous species and herbivorous species is needed to confirm this hypothesis. Whether species have an omnivorous, carnivorous, granivorous or grazing diet is shown in Table 2.

Which resources are foraged on by dabbling ducks when the most preferred resource is scarce, or when competition is high, is linked to the morphological features of the species (e.g. bill shape, lamellar density and body length). Therefore it was attempted to find a correlation between bill shape and diets consumed by different species of dabbling ducks. Though an association was found between bill shape and different diets, (where four different bill shapes were related to four types of diets; granivorous, grazing, omnivorous, and carnivorous) there were also some exceptions to this rule (Table 2). For example the yellow-billed teal (*A. flavirostris)* seems to have a bill shape that is more adjusted to ingestion of seeds, however this species mainly consumes invertebrates (del Hoyo *et al.*, 1992). Another example is the Auckland teal (*A. aucklandica*), who's bill seems to be shaped for an omnivorous diet, however this species also mainly consumes invertebrates (del Hoyo *et al.*, 1992). Finally there is the red shoveler (*A. platalea*), which seems to have a bill shape adapted to a diet containing high amounts of invertebrates, however this species mainly consumes seeds (del Hoyo *et al.*, 1992).
This dissimilarity between bill shape and diet could have arisen if these species had different diets before, and "recently" turned to other diets. If this is the case, their bill has not had time to adjust to the new diets. This is probably what happened with pintails and gadwalls, which used to have a more limited diet than they have nowadays. Before there were agricultural crops, the pintail fed on small seeds and the gadwall on aquatic plants. Therefore, they still have narrower bills than the mallard (Davis, www.ducks.org).

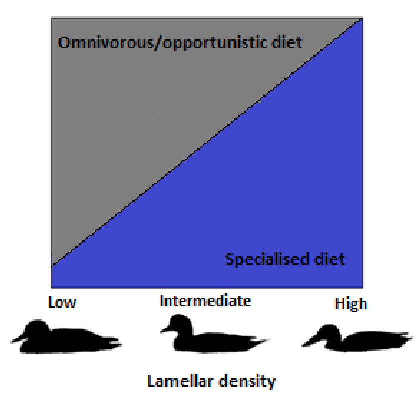


Figure 6. Schematic representation of the relationship between lamellar density and amount of diet-specialisation. From left to right, silhouettes from mallard, American wigeon and northern shoveler. Silhouettes adapted from www.nwbackyardbirder.blogspot.nl

Differences in lamellar densities between different species of dabbling ducks were also analysed. Results indicated that there might be a relationship between the lamellar density and how specialised a species is. Species with larger inter-lamellar spacing seem to be less specialised than species with smaller inter-lamellar spacing (Table 2). Despite the fact that the lamellar densities of many species were not reported in literature, the species from which the densities have been found are very diverse, making it possible to discover certain relationships. Table 2 shows that the lamellar density is highest in the northern shoveler and common teal. These two species are highly specialised in terms of their diet. The northern shoveler primarily consumes invertebrates, while the common teal is specialised in consumption of seeds. The lamellar density was lowest in the mallard, which is a generalist and opportunistic species (del Hoyo *et al.*, 1992). Figure 6 shows a schematic hypothetical representation of the relationship between lamellar density and the amount of specialisation.

Differences in the amount of specialization probably lead to differences in dispersal of aquatic organisms. For example, species specialised in consumption of seeds will probably disperse higher amounts of plant seeds than species specialised in consumption invertebrates. Less specialised (omnivorous/opportunistic) species probably disperse a higher variation of aquatic organisms than more specialised species. Furthermore, species with higher lamellar densities will be able to disperse both small and larger propagules, while species with lower lamellar densities probably disperse a lower amount of smaller propagules (Nudds & Bowlby, 1984; Nudds, 1994; Brochet et al., 2012).

In addition to the lamellar density, different diets between dabbling duck species depend on body-length (Guillemain *et al.*, 2002; Pöysä, 1983). Table 2 shows that different dabbling duck species are highly variable in terms of body length. Duck species with a longer body (e.g. northern pintail, mallard, meller's duck etc) are capable to reach food sources that are in deeper parts of the water than species with shorter body lengths (e.g. common teal, garganey, hottentot teal etc.). Therefore, dabbling duck species with different body lengths might disperse different aquatic organisms. Species with longer bodies can disperse aquatic species that are in deeper parts of the water than duck species with a shorter body. Figure 7 shows the relationship between body length and foraging depth.

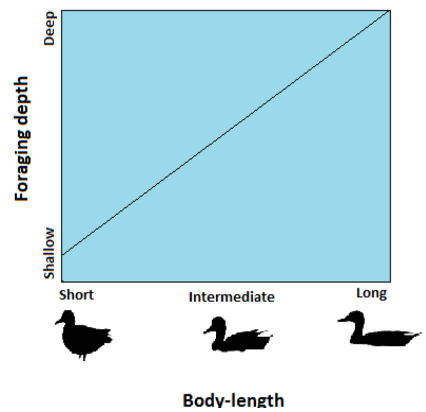


Figure 7. Relationship between body length and foraging depth. From left to right, silhouettes from common teal, gadwall and northern pintail. Silhouettes adapted from www.nwbackyardbirder.blogspot.nl

Beside different diets of varying duck species, differences in dispersal of aquatic organisms could also be influenced by differences in passage through the digestive tract. Variations in retention time between different duck species might result in varying dispersal distances. However, during this study, it was shown that inter-specific differences between seeds of plant species are more important factors determining gut passage time and germination success than inter-specific differences between digestive tracts of different dabbling duck species. Because GRT values between many dabbling duck species are highly similar (Charalambidou *et al.*, 2003), it can be concluded that differences in dispersal of aquatic organisms between different species of dabbling ducks are probably the result of different diets and differences in behaviour (migration patterns) and not from differences in the digestive tract (Viana *et al.,* 2013).

Even though different species of dabbling ducks are probably highly similar in terms of gut physiology, van Leeuwen *et al.* (2012a) found that the amount of dispersal of aquatic organisms is slightly higher in ducks with a higher body mass. Table 2 shows that there is a high variation in body masses between different dabbling duck species, ranging from 216 g (hottentot teal), to 1350 g (American black duck). However, since species with larger body-masses often contain a lower dropping rate (Hahn *et al.*, via van Leeuwen *et al.*, 2012 a), the effect of body-mass is likely to be nullified. Further investigation is needed to determine whether there is really an effect of body mass on dispersal patterns.

Another factor that might be important to determine where ingested propagules will end up and how far they might be dispersed are differences in movement patterns between species of dabbling ducks. However, movement patterns do not only vary between dabbling duck species (Table 2), but they might also vary within species. For example, they vary between different ages of the individuals and between sexes (Lurz *et al.*, 2002).

Whether or not ducks migrate is to a large extend dependent on the latitude where they breed (Newton & Dale, 1996a; Newton & Dale, 1996 b). In Table 2 it can be seen that duck species from higher latitudes tend to be more migratory (e.g. garganey, northern shoveler and northern pintail), these species move to lower latitudes during winter. Ducks breeding in lower latitudes (in tropical zones) are generally more sedentary (e.g. African black duck, Philippine duck and white-cheeked pintail). This indicates that duck species from higher latitudes are probably able to disperse aquatic organisms over larger distances than duck species from lower latitudes. Figure 8 shows a hypothetical interpretation of the relationship between latitude and migration strategy. At the poles, the number of migrating ducks will be zero, or close to zero, since (virtually) no duck species occur above the polar circles. Then the number of migrating ducks strongly increases below the polar circles, where the winters are very harsh. Closer to the equator, the number of migrating ducks decrease due to the more temperate climates. Around the equator, in the tropical zones, almost no duck species make long distance migrations. Furthermore, the number of migrating duck species is lower on the southern hemisphere, because (due to a smaller land mass) there are less duck species on the southern hemisphere than on the northern hemisphere.

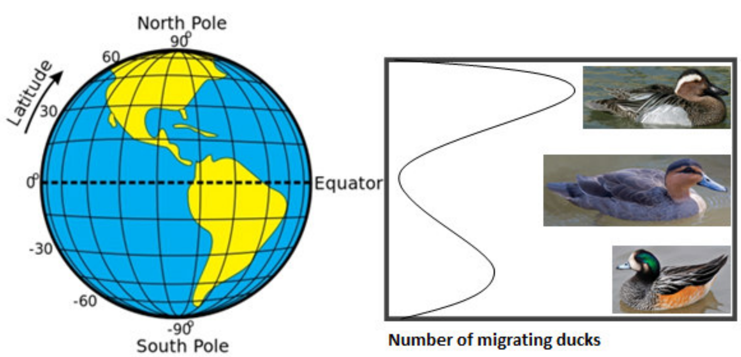


Figure 8. Hypothetical relationship between latitude and number of migrating dabbling ducks. Duck species on the right are categorized according to the latitude they come from. Duck species from top tom bottom: Garganey (*A. querquedula*) from higher Northern latitudes, Phillipine duck (*A. luzonica*) from tropical regions, Chiloe wigeon (*A. sibilatrix*) from higher Southern latitudes. Picture of globe from www.avontrail.ca. Pictures of ducks from (top to bottom): http://en.wikipedia.org, http://www.ontfin.com, http://www.flickr.com

Besides long distance movements, short distance movements are also important for the dispersal of aquatic organisms. Duck species with high amounts of local movements will probably be more important for the dispersal of aquatic organisms on a local scale than duck species with lower amounts of local movements. In order to determine how important short-distance movements are, it should be investigated whether there are differences in local movements between different species of dabbling ducks, and how these different movements influence the dispersal of aquatic organisms.

The impact certain duck species have on the dispersal of aquatic organisms depends on the population size of that species. Different dabbling duck species contain a high variety of population sizes (Table 2). It can be assumed that species with a larger population size disperse more individuals and species of aquatic organisms than species with smaller population sizes. However, since even highly endangered duck species might be important for the dispersal of aquatic organisms on a local scale, more knowledge about the importance of these duck species for the dispersal of aquatic organisms might lead to stricter conservation measures of these species.

Priorities for future research

Even though there are many publications about dispersal of aquatic organisms by dabbling ducks, there are still some uncertainties. It is not yet certain how excretion of aquatic organisms is influenced by the different diets consumed by different duck species, how important local movements are for the dispersal of aquatic organisms between wetlands nearby, whether there is a correlation between body-mass and the amount of endozoochorous dispersal of aquatic organisms, or why smaller particles have higher chances of successful germination and are retrieved more often after ingestion than larger particles. Furthermore, more species and individuals of dabbling ducks need to be investigated to figure out whether they are all capable of active selection of particles by size. Finally, it has to be investigated in the field whether long-distance dispersal is influenced by differences in migration strategies.

Until now, many studies focussed on the importance of more common duck species for the dispersal of aquatic organisms. For future research it is important that the impact of endangered duck species on the dispersal of aquatic organisms within and between wetlands is also investigated. First of all, because it will be too late to investigate this once these species are extinct. Second, more knowledge about the importance of endangered duck species could lead to better measures to protect them.

It can be concluded that more knowledge about the vectors regulating dispersal of aquatic organisms between wetland areas might not only lead to better measures to conserve wetlands, but it might also lead to stricter measures to protect endangered duck species.

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