Speeding up the snail's pace: bird-mediated dispersal of aquatic organisms
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English summary

Movement of species in the landscape is essential for the long term survival of their populations. Nearly all species are therefore capable of dispersing within and between suitable habitats. However, the earth's landscape is heterogeneous and includes many ecological barriers that restrict such movements. To cross these barriers species may travel by own propulsion, or can make use of vectors such as wind, water or other animals to disperse. Aquatic species that are bound to freshwater wetlands are often considered to live on "islands in a sea of land", with land forming a major barrier for their dispersal. Since many small aquatic species lack the ability to disperse long distances by own propulsion, it is interesting and important to investigate vector-mediated dispersal in these systems.

Inspired by the long standing suggestion of Darwin that especially waterbirds may be important dispersal vectors in aquatic systems, this thesis explores bird-mediated dispersal of aquatic organisms. Waterbirds travel fast and in large numbers between similar wetlands, and are therefore increasingly recognized as important dispersal vectors in aquatic systems. They may carry propagules of aquatic organisms either internally in their gut (endozoochory) or externally on their bill, feet and feathers (ectozoochory). The thesis starts with exploring the current knowledge on internal transport in a meta-analysis, followed by experiments on internal and external transport and genetic analyses to detect potential effects of bird-mediated dispersal on populations.

The meta-analysis in **Chapter 2** reviews all currently available peer-reviewed publications on waterbird endozoochory of freshwater plant seeds and macro-invertebrates. As many as 17 species of Anatidae and Rallidae are involved in dispersing at least 39 species of macro-invertebrates and 97 species of plant seeds. On average, one-third of all investigated waterbird droppings contains one or more intact propagules of an aquatic organism. One-third of these propagules is also viable and can thus potentially establish in a new habitat after transport. The literature-extracted data is used to describe a model with which the number of propagules carried by birds can be calculated between any wetlands of interest. This model indicates that the average bird disperses five viable propagules after flying more than 100 km, and one additional propagule after flying the subsequent 200 km. The wide variety of aquatic plants and macro-invertebrates that can be dispersed can be explained by the fact that birds maximize their energy intake over time, rather than their digestive efficiency itself. The associated relatively low digestive efficiency of ~70% provides an opportunity for many small species to be dispersed by endozoochory.

The suggestion that many aquatic species are able to use this digestive trade-off for their dispersal is further supported by our finding that aquatic snails (Gastropoda) can pass the guts of birds alive (**Chapter 3**). One of four snail species that we fed to mallards (Anas *platyrhynchos),* i.e. *Hydrobia* (Peringia) *ulvae* (Hydrobiidae), can survive up to five hours in the digestive tract of mallards. This resembles a maximum potential bird-assisted dispersal distance in excess of 300 kilometres and indicates that endozoochory may indeed be a widespread mode of dispersal. Although aquatic snails are adapted to survive in a variety of environmental circumstances and extreme conditions, they are not known to be specifically adapted for endozoochorous transport by birds. This further supports the view that bird-mediated dispersal may be possible for a wide variety of species, including those lacking specific adaptations for endozoochory.

A common problem of experiments performed to estimate potential endozoochorous dispersal distances is that they are conducted on resting animals, whereas animal vectors in natural situations will always be actively moving during effective transport of propagules. The effect of physical activity of vectors on the release pattern and dispersal efficiency of propagules is addressed in **Chapter 4**. Digestive characteristics between mallards that are swimming, wading (i.e. resting in water) and resting in a cage were compared. Retention times of markers appear to be shortened by approximately one hour (to five hours and 20 minutes) in the swimming compared to the resting mallards, and by half an hour (to six hours) in wading birds. This implies that active birds release propagules at shorter dispersal distances than previously inferred from experiments with resting birds and mammals in both aquatic and terrestrial systems. Faster retrieval of propagules indicates shorter dispersal distances, but also higher propagule survival because viability of propagules decreases exponentially with increasing retention time. In this experiment we also vary marker size, which reveals that smaller markers were retrieved faster than larger

markers. This indicates smaller propagules may be dispersed over shorter distances but have higher survival potential.

Whereas our experiments and meta-analysis show that aquatic species have the potential to be dispersed internally by endozoochory, they may also be carried externally on birds. Our complementary experiments that we describe in **Chapter 5** indicate that aquatic snails have many of the necessary prerequisites for successful transport by external adhesion to birds. They readily attach to birds and can remain attached to the bills of mallards in drying mud for up to eight hours. All snail species that we tested survived aerial exposure over 48 hours, which would be sufficient for dispersal over long distances. The experiments indicate that snails have ample potential for bird-mediated dispersal, and that ectozoochory can be another important mechanism explaining the wide distributions of many aquatic species. However, further assessment of the capacity of snails (and other propagules) to stay attached to birds during flight remains an interesting future challenge.

Although experiments provide valuable information on the potential of snails and other propagules to be transported by waterbirds, these can not confirm that actual dispersal also occurs in field situations and has consequences at the metapopulation level. We therefore also investigate the dispersal of aquatic snails by waterbirds using molecular genetic techniques. The genetic population structure of two focal species, i.e. *Physa acuta* (Physidae) and *Galba truncatula* (Lymnaeidae), is analysed with regard to dispersal. Small scale dispersal of snails (tens of kilometres) is investigated with *Physa acuta,* an invasive species in Europe that originates from North America. This species is found to occur in many isolated, temporary ponds in Doñana National Park, Southern Spain. Microsatellite markers indicate the contribution of multiple dispersal vectors to the distribution of this species (**Chapter 6**).

Genetic analyses supported the idea that *P. acuta* exploits water connections, birds and also large mammals as vectors in this system. This highlights how multiple dispersal vectors are together important for the overall wide distribution of this species and its success as an invasive species. Whether bird-mediated dispersal also has the potential to affect species distributions on the scale of thousands of kilometres is addressed by analysing the distribution and phylogenetic position of *Galba truncatula* in **Chapter 7**. This snail is an important vector for livestock and human parasites and can be found on the Eurasian, African, Northand South-American continents. Analysing its distribution in detail reveals its presence on at least 14 islands and 14 highland areas. This distribution has many similarities with the major migratory flyways of (water)birds, suggesting birds may also be vectors for this species. The phylogenetic position of *G. truncatula* suggests that it has an American origin and that birds may have introduced this species into Europe after the separation of the Eurasian and American continents. Birds may have carried this snail and its associated parasites over thousands of kilometres in the past and may continue to be important for its dispersal.

In conclusion, the research in the thesis indicates that many aquatic plants and invertebrates can be dispersed by waterbirds internally and a series of aquatic snail species have at least the necessary prerequisites for external transport. This dispersal may not only affect the occurrence of species on a local scale, but can also influence their worldwide distribution. Bird-mediated dispersal significantly contributes to species' survival, to the biodiversity of wetlands and can help small aquatic organisms to cope with a changing environment. In the synthesis of this thesis, **Chapter 8**, this knowledge on bird-mediated dispersal is compared to dispersal by other potential vectors in aquatic systems. Waterbirds are quantitatively less important than transport by wind and water, but far more effective when it comes to transporting species between suitable habitats. Birds readily fly across major ecological barriers such as land or oceans, traveling fast and directed between similar wetlands in large numbers. The fact that they importantly contribute to sustaining a wide variety of other aquatic species in wetlands around the globe once more indicates that care should be taken to protect these important players in aquatic ecosystems.