

SYNTHESIS



Gut travellers: internal dispersal of aquatic organisms by waterfowl

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ABSTRACT

Aim Patterns of high biodiversity among less mobile organisms throughout isolated locations suggest that passive dispersal importantly contributes to biodiversity. We examined the contribution of waterbirds to the dispersal of plant seeds and macroinvertebrates between aquatic wetlands. Birds are renowned vectors for seeds of terrestrial plants, but less is known about their role in more dispersal-dependent aquatic systems. We therefore performed a meta-analysis on bird-mediated endozoochorous dispersal of aquatic species.

Location Our review included studies that collected data world-wide.

Methods We analysed data from 81 peer-reviewed publications on endozoochorous dispersal of aquatic plant seeds and macroinvertebrates by waterbirds.

Results In total, 36% of 1581 waterbird droppings collected in the field contained one or more intact propagules, with macroinvertebrates found almost as frequently as plant seeds. Positive droppings contained on average 3.3 intact propagules, of which one-third were viable. In 728 trials from 17 published feeding experiments 24% of the ingested propagules were retrieved intact, with *c.* 6.5% both viable and intact. As many as 17 species of Anatidae and Rallidae were involved in the dispersal of at least 39 species of macroinvertebrates and seeds from 97 species of plants across a wide taxonomic range. Smaller propagules seemed less affected by digestion than larger ones. We provide a first quantitative model that can be used to estimate waterbird-mediated dispersal of propagules between wetlands. This model indicates that an average waterbird has the potential to disperse five viable propagules after flying more than 100 km, and one additional propagule after flying 300 km.

Main conclusions We demonstrate that waterbirds have the potential to transport a wide variety of aquatic plants and animals over several hundreds of kilometres. High survival of propagules might be explained by propagule adaptations or by the digestive adaptations of birds, whereby energy absorption is thought to be maximized rather than assimilation efficiency. Our meta-analysis suggests that waterbirds might contribute significantly to wetland biodiversity around the world, despite several limitations to our current knowledge. We outline avenues for future research to address these knowledge gaps.

Keywords

Anatidae, aquatic propagules, digestive physiology, long-distance dispersal, macroinvertebrates, plant seeds, Rallidae.

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INTRODUCTION

The presence of sessile organisms at remote and isolated locations in the landscape has fascinated scientists for over a century (Darwin, 1859; Ridley, 1930; Gittenberger *et al.*,

2006). Species distributions often range across geographical barriers, such as deserts and oceans (Schabetsberger *et al.*, 2009; Jocque *et al.*, 2010), suggesting high species mobility in the landscape (Lester *et al.*, 2007). However, for many species it is still unknown how, and how often, they disperse

between these remote habitats (Cain *et al.*, 2000). Understanding of potential modes of dispersal and dispersal frequency is essential for understanding (meta)population functioning and community dynamics (Puth & Post, 2005), and forms the basis for understanding the movement of invasive species and species threatened by habitat fragmentation or global change (Kokko & López-Sepulcre, 2006).

Islands provide excellent model systems with which to study dispersal and metapopulation dynamics because of their discrete character (MacArthur & Wilson, 1967; Gillespie *et al.*, 2008). Wetlands, which can be considered 'islands in a sea of land' (C. Darwin in Darwin, 1909), are particularly suitable to study dispersal of aquatic organisms. Many wetlands are isolated from other aquatic areas, yet still harbour a high biodiversity of aquatic organisms. This apparent paradox prompted Darwin (1859) to hypothesize that waterbirds may be responsible for the dispersal of less mobile aquatic organisms over land. Indeed, analogous to how frugivorous birds disperse terrestrial plant seeds and fruits (e.g. Mazer & Wheelwright, 1993; Traveset, 1998), waterbirds disperse aquatic propagules. Anatidae (ducks, geese and swans) and Rallidae (coots, rails, gallinules and crakes) thereby not only carry small propagules such as algal spores (Schlichting, 1960; Kristiansen, 1996) and viruses (e.g. Winker & Gibson, 2010), but also larger aquatic plant seeds and macroinvertebrates that either survive in their digestive system (endozoochory) or adhere externally (ectozoochory).

The frequent, directed movements of waterbirds between ecologically similar wetlands make them particularly suitable transport vectors (Figuerola & Green, 2002; Green *et al.*, 2002; Bohonak & Jenkins, 2003; Nathan *et al.*, 2008), especially relative to more random dispersal by vectors such as wind (Jenkins & Underwood, 1998; Soons, 2006), unidirectional water flows limited to river channels or flood occurrence (Jacquemyn *et al.*, 2010; Pollux, 2011), irregular anthropogenic activities (Wichmann *et al.*, 2009; Waterkeyn *et al.*, 2010; Kappes & Haase, 2011) or slower, less abundant non-avian animals (Bilton *et al.*, 2001; Vanschoenwinkel *et al.*, 2008). However, to estimate their quantitative importance as dispersal vectors, we need to be able to estimate how many propagules are dispersed by which birds. Although earlier reviews have importantly addressed qualitative dispersal of aquatic seeds and invertebrates by waterbirds (Bilton *et al.*, 2001; Figuerola & Green, 2002; Malmqvist, 2002; Okamura & Freeland, 2002; Bohonak & Jenkins, 2003; Green & Figuerola, 2005), little is known on the quantitative importance of bird-mediated dispersal.

We therefore present a quantitative meta-analysis on endozoochorous transport of aquatic organisms by waterbirds. Because data on ectozoochory remain extremely limited we focus only on endozoochory. We test whether the capacity of waterbirds to disperse propagules differs between dabbling ducks, diving ducks and coots, and if this can be explained by their physiological characteristics. We compare the dispersal potential of aquatic macroinvertebrates to the more intensively studied dispersal of aquatic plant seeds (e.g. Charalambidou &

Santamaría, 2002). By including data from both experimental studies and field studies, we present a first estimate of the percentage of ingested propagules that survive gut passage of birds, which we use to construct a quantitative dispersal model that indicates propagule release by birds over time. We conclude by comparing the success of differently sized propagules and postulating explanations for why birds disperse aquatic propagules. Future directions for research on this mode of dispersal are indicated throughout the manuscript.

MATERIALS AND METHODS

Data collection

We reviewed a total of 81 peer-reviewed publications referring to bird-mediated dispersal in freshwater habitats to date (listed in Appendix S1 in Supporting Information). Literature was collated by searching databases ISI, PubMed, Scopus and Google Scholar. Search terms included 'dispersal', 'waterbirds', 'water fowl', 'endozoochory', 'internal transport', and combinations of these, as well as references cited by these results. Most publications from before *c.* 1980 were retrieved from the Zoological Record and library databases of Dutch universities as well as the literature archive of NCB Naturalis, Leiden, The Netherlands.

The analysis was restricted to endozoochorous dispersal of freshwater macroinvertebrates (> 0.5 mm) and aquatic and semi-aquatic macrophyte propagules (mainly angiosperm seeds, but including liverwort spores and Characeae oogonia) found in or on the shores of freshwater habitats. Species from brackish and saline habitats were excluded, except for the well-studied, salt-tolerant *Ruppia maritima*. We focused on the avian families Anatidae and Rallidae as vectors, reviewing their capacity to disperse propagules by ingestion, transport and release in droppings. Publications on the external transport of invertebrates and seeds by birds were excluded. Geese were predominantly implicated in the dispersal of terrestrial seeds (Willson *et al.*, 1997; Chang *et al.*, 2005; Bruun *et al.*, 2008) and were thus not included.

We classified the diet of each bird species, distinguishing between predominant omnivores and predominant herbivores using Bruinzeel *et al.* (1997), Nummi & Vaananen (2001) and Dessborn *et al.* (2011). Birds that are known to forage deliberately on animal matter were considered omnivorous, and those only known to forage on plant material as predominantly herbivorous. Because the diets of Anatidae and Rallidae can vary with season and food availability (e.g. Guillemain *et al.*, 2007; Arzel *et al.*, 2009) we distinguish only predominant feeding guilds, acknowledging that some herbivores may feed opportunistically on invertebrates from time to time and vice versa.

Meta-analysis data

From the 81 publications reviewed, we found: (1) nine anecdotal publications in which bird-mediated dispersal was

merely indicated as a possible dispersal mechanism or evidence consisted of a single observation; (2) 23 publications in which dispersal by birds was inferred or suggested on the basis of the distribution patterns of aquatic species or analyses of their genetic variability; (3) 30 publications describing endozoochory experiments – waterbirds were fed a known amount of propagules and retrieval was monitored; (4) 16 published observations from dropping collections in the field; and (5) 18 previously published reviews related to dispersal by waterbirds potentially of interest to readers interested in transport of aquatic propagules by birds. Three additional publications contained data for both categories (3) and (4). All publications used are indicated in Appendix S1, and included European, North American and Australian birds and propagules.

Data for the meta-analysis was extracted from publications in categories (3) and (4). A total of 17 publications from category (3) carried out propagule feeding experiments in a comparable way, and provided a detailed description of the methods and results that allowed pooling the data for the meta-analysis (see Appendix S1 for details on the excluded publications). A total of 668 trials with dabbling ducks, 38 trials with diving ducks and 22 trials with Rallidae (total 728, of which 387 were with mallards, *Anas platyrhynchos*) are published to date. The setup of studies varied on the basis of the availability of food during the experiments, time of the year studies were conducted, bird species used, each of which we either included explicitly in the statistical models or considered in the discussion. From all studies we extracted the number of experimental birds per species, the number of propagules fed to these birds, the percentage of propagules retrieved in total during the experiment, and the percentage of these retrieved propagules that was viable (tested after 94% of the trials in 14 of the 17 studies). Six of the studies reported passage rates of 281 feeding trials at 4-h intervals, of which we additionally extracted 4, 8 and 12 h retrievals.

Nine publications in category (4) collected fresh droppings from Anatidae or Rallidae and examined their contents in a comparable way (indicated in Appendix S1). Collectively, these studies examined 1581 droppings from 14 different bird species. From these publications we extracted the number of droppings examined, the number of droppings containing at least one propagule, the number of propagules per dropping, and the percentage of propagules that was viable for each bird species that was investigated. Publications investigating lower gut contents rather than dropping contents were included in the taxonomic identification of dispersed species, but were not included in the quantitative analyses as the number of propagules per dropping remained unknown.

Calculations of the quantitative dispersal model

The collected data allowed us to calculate a first quantitative estimate of the average number of propagules dispersed by

waterbirds over time. We therefore combined the average number of propagules per dropping, their viability, bird dropping rates and retention times of ingested propagules. We used our findings in the meta-analysis to estimate the average number of propagules per dropping, and modelled propagule viability as decreasing exponentially with increasing retention time, dropping rates as a range of 2.4 to 9.7 droppings per hour, and propagule release as decreasing exponentially over time (see Appendix S2 for details on the model and the publications on which the here mentioned estimates are based).

Statistical analyses

The influence of physiological and anatomical differences between Anatidae and Rallidae species on their ability as dispersal vectors was tested using two generalized linear models and functions in R (R Development Core Team, 2011). The average number of propagules per dropping (square-root transformed) followed a Poisson distribution and was modelled using a quasi-Poisson error function to correct for non-integer values, with log link function using 'glm' of package 'stats'. The viability of propagules was analysed with a binomial error distribution with log link function, using function 'lm'. The number of droppings examined was included as a weighting factor in both models, because the more droppings collected, the more accurate the estimate of number of propagules per dropping. Body mass, gizzard mass and gut length of the birds were extracted from the literature and included as centred covariates. As these covariates were unique per bird species, bird species could not be included in the models as an additional factor. Because most studies only included a single or limited number of species, the inclusion of study as a random factor inhibited the detection of effects of covariates. Species effects were thus analysed between rather than within studies. For this reason, results should be treated with caution, given that the differences in methodology between studies have not been statistically accounted for. Interactions and the fixed factors feeding guild and 'subfamily' (i.e. diving duck, dabbling ducks or Rallidae) were not included because they resulted in over-determination of the models. The effect of propagule size on the percentage of retrieved propagules during experiments was modelled after square-root transformation of this percentage, using the linear regression function 'lm'.

RESULTS

Propagules collected in the field and during experiments

Plant propagules were present in 45.4% of 1293 dropping investigated for plant seeds. Invertebrate propagules were present in 32.3% of the 975 droppings that were investigated for invertebrates. This percentage of positive droppings was not statistically different between plants and macroinvertebrates

($W = 1055$, $P = 0.06$). Of all the droppings that were found to contain at least one propagule, an average of 3.32 (± 0.70 SE) intact propagules were present (plants: 2.85 ± 0.70 SE, invertebrates: 3.75 ± 1.16 SE, $W = 783$, $P = 0.89$). Of the droppings for which propagule viability was tested (711 droppings, i.e. for 53% of all droppings the viability of retrieved propagules was determined), 35.8% of the plant propagules and 30.3% of the macroinvertebrates were viable with no significant difference between plants and invertebrates ($W = 159$, $P = 0.17$). On average, c. 12% of all droppings collected contained either one viable plant seed or one viable macroinvertebrate propagule (Fig. 1a,b).

In the six experimental studies that reported passage rates at 4-h intervals based on 281 feeding trials, on average 68.1% (± 19.7 SD) of all retrieved propagules were excreted within 4 h, 85.0% (± 14.7 SD) within 8 h and 92.3% (± 10.8 SD) within 12 h. Across all comparable studies, 23.5% of the ingested propagules were retrieved intact, of which 27.9% were viable. This indicates that experimentally, roughly 6.5% of the initially ingested propagules were retrieved both intact and viable. Quantitative data from the field collections and experiments were combined and used to construct a model indicating propagule release by birds over time (details on the model can be found in Appendix S2, the result is depicted in Fig. 2).

Taxonomy of dispersed aquatic propagules

To date, 39 species of macroinvertebrates and 97 species of wetland plants have been found capable of bird-mediated dispersal by endozoochory (Appendix S3). The number of species per family that have been identified as being capable of endozoochorous dispersal by birds correlated with the number of publications that tested this ($r = 0.75$). During experiments, smaller propagules were retrieved in significantly larger quantities (Fig. 3), although this relationship could only explain a small portion of the variation in propagule recovery ($R^2 = 0.12$). While 95% of the data in this analysis comprised experiments in which plant seeds were fed, the available macroinvertebrate data showed a similar trend (Fig. 3).

Differences between bird species as vectors

Diving ducks (Aythyinae), dabbling ducks (Anatinae) and Rallidae (predominantly *Fulica atra*) did not differ in their quantitative dispersal capacity based on the limited dropping collection data currently available. The (sub)families had on average 3.4 (± 5.0 SD, $n = 79$ droppings), 3.6 (± 7.4 , $n = 1028$) and 2.1 (± 3.4 , $n = 450$) propagules per dropping, respectively, and overlapped in their capacity to disperse certain species. Qualitatively, dabbling ducks have been found to disperse more invertebrate and plant species (Table 1), but this pattern does not hold when the number of droppings investigated is also taken into consideration (diving

ducks: c. 4 droppings investigated per identified species, dabbling ducks: c. 10 droppings per species, Rallidae: c. 20 droppings per species). Not all aquatic species dispersed by diving ducks and Rallidae were also dispersed by dabbling ducks, as indicated by the overlap in Table 1.

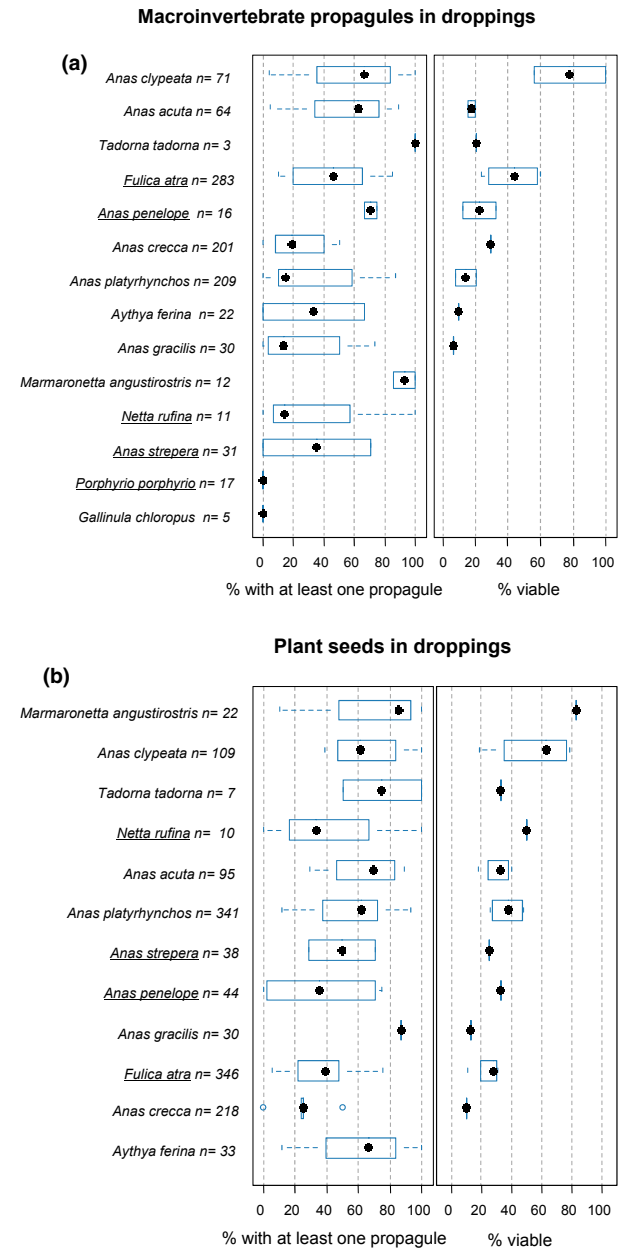


Figure 1 Percentage of droppings with at least one (a) intact macroinvertebrate propagule or (b) seed, and the percentage of these propagules that was viable (based on collections of droppings in the field only). On the vertical axes bird species are ranked according to decreasing quantitative dispersal capacity, calculated from both the prevalence and viability of propagules in their droppings. n denotes the number of droppings collected. Underlined species are considered predominantly herbivores.

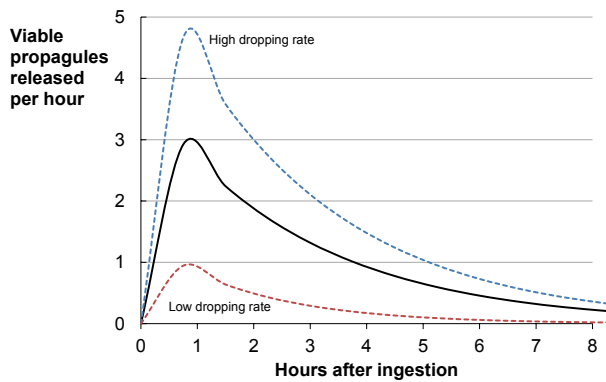


Figure 2 The potential number of viable propagules excreted by waterbirds per hour based on feeding experiment data extracted from the literature. Dropping release over time was calculated by (dropping release = $e^{2.465 - T^{0.196}}$, with T representing time in hours since ingestion of a propagule). Viability was found decreasing exponentially over time according to (percentage of propagules viable = $e^{3.938 - T^{0.0688}}/100$, with T representing time in hours since ingestion). The number of viable propagules dispersed at time T was then calculated by (dropping release * percentage of propagules viable). The upper and lower dashed lines represent bird species with high and low dropping rates, respectively, compared to average dropping rates (solid line).

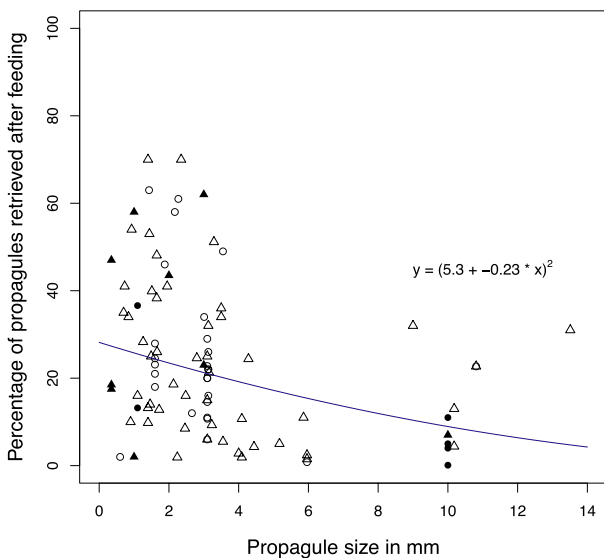


Figure 3 The total percentage of ingested propagules retrieved intact after feeding to waterbirds over the duration of experiments was lower for larger propagules (linear regression: $F_{1,89} = 12.6$, $P < 0.01$, $R^2 = 0.12$). Effect size of propagule size on the square-root scale was -0.23 ± 0.065 SE. The linear regression over the square-root-transformed data is depicted on the normalized scale for clarity of percentages. Open symbols denote plant seeds, and closed symbols macroinvertebrate propagules. Fifty-three per cent of the experimental birds were mallards (triangles), circles are other duck and Rallidae species. The regression was also significant for mallards only, as well as for all other species excluding mallards.

Viability of propagules was similar between the avian (sub)families based on the currently available data, with 48% of the propagules from diving ducks found viable ($n = 45$

Table 1 Number of plant and invertebrate species known to be dispersed by different waterbird vectors grouped by (sub)family, including overlap between (sub)families, based on both feeding experiments and dropping collections in the field.

Vector species	(Sub)family	No. of invertebrate species	No. of plant species
Unspecified 'waterbirds'		17	2
<i>Anas acuta</i>	Dabbling	5	6
<i>Anas carolinensis</i>	Dabbling	1	3
<i>Anas clypeata</i>	Dabbling	9	4
<i>Anas crecca</i>	Dabbling	6	26
<i>Anas penelope</i>	Dabbling	3	3
<i>Anas platyrhynchos</i>	Dabbling	19	61
<i>Anas strepera</i>	Dabbling	4	2
<i>Anas superciliosa</i>	Dabbling	1	4
Dabbling ducks, total variety		24	80
<i>Aythya affinis</i>	Diving	1	0
<i>Aythya collaris</i>	Diving	0	3
<i>Aythya ferina</i>	Diving	4	2
<i>Marmaronetta angustirostris</i>	Diving	5	8
<i>Netta rufina</i>	Diving	2	3
Diving ducks, total variety		8	11
<i>Fulica atra</i>	Rallidae	9	13
<i>Porphyrio porphyrio</i>	Rallidae	1	4
Rallidae, total variety		9	15
Overlap dabbling and diving		4	10
Overlap Rallidae and diving		5	5
Overlap Rallidae and dabbling		7	10

droppings), 34% from dabbling ducks ($n = 772$) and 34% from Rallidae ($n = 379$). The viability of propagules (Fig. 1a, b) was on average 32% for herbivores ($n = 453$) and 34% for omnivores ($n = 743$), with $2.0 \pm SD 3.4$ and $3.9 \pm SD 7.2$ propagules per dropping, respectively. However, note that droppings of species considered as herbivores also contained invertebrate propagules (Table 1).

Digestive physiology and anatomy

Birds with a higher body mass and smaller gizzard mass excreted more propagules per dropping (GLM: $F_{3,48} = 14.4$, $R^2 = 0.47$ for the entire model; body mass: $P < 0.01$, effect size = 0.19 propagules per dropping per 100 g increase in bird body mass; gizzard mass $P < 0.04$, effect size = -0.005 propagules per dropping with a 1 g increase of gizzard mass; no effect of gut length). There was also a small positive effect of bird body mass on viability of the excreted propagules, after removing insignificant effects of gizzard mass and gut length (log regression: $F_{1, 64} = 6.05$, $R^2 = 0.09$ for the entire model; body mass: $P < 0.02$, 1.4% more chance of retrieving a viable propagule per 100 g increase in bird body mass).

DISCUSSION

Waterbirds were found to disperse a wide variety of aquatic organisms by endozoochory, with more than twice as many

plant (97) as macroinvertebrate species (39) implicated in this dispersal process (Appendix S3). One-third of all droppings that were collected in the field and investigated in published studies contained at least one propagule, of which one-third were also viable. Considering the limited number of studies that have addressed this topic to date, the number and taxonomic range of aquatic propagules that may be endozoochorously dispersed is potentially quite large. The strong correlation between the number of species identified as having the potential to be dispersed and the number of publications investigating these same species suggests additional work on other organisms will also reveal additional organisms with the propensity for endozoochorous dispersal. The fact that macroinvertebrates were found to be as abundant in droppings as plant seeds, despite a lower research effort, indicates that studies on this taxonomic group may be most rewarding in future investigations.

Model for quantifying propagule release over time

As a first step towards assessing the quantitative importance of dispersal by waterbirds, the quantitative dispersal model (Fig. 2, Appendix S2) indicates that if an average waterbird flies at a speed of 75 km h^{-1} (Welham, 1994; Bruderer & Boldt, 2001; Clausen *et al.*, 2002; Miller *et al.*, 2005) for prolonged time, it has the potential to disperse five viable propagules after flying more than 100 km, and one additional propagule after flying 300 km. Thereby the realized dispersal will depend on more factors than incorporated in the model at this stage. Nevertheless, the model could provide an indication of the number of propagules transported by waterbirds with known foraging and flight behaviour. For instance, the potential connectivity of two wetlands on a migratory route could be calculated based on the distance between these wetlands and the number of birds that visit both sites each year during migration. Likewise, transport of a propagule species to an island could be estimated if the number and location of birds foraging on the mainland was known. However, the model provides an estimate rather than an exact value, and relevance to specific field situations would require additional validation.

Variation between birds as vectors and where to concentrate future effort

Variation in investigation effort between bird species and between propagule species can lead to the conclusion that certain birds only disperse certain propagules (Appendix S3). However, such indications can be predominantly attributed to differences in investigation effort. The majority of experimental trials and field collections focused on dabbling ducks (and notably mallards), resulting in a clear bias in both the vector species investigated (Table 1) and the number of droppings investigated per bird species (Fig. 1a,b). Our review therefore provides a clear assessment of the least investigated species, and those requiring additional research

effort. Diving ducks may be of special interest, because the number of identified species per investigated dropping was highest, despite the relatively small investigation effort. Both diving ducks and Rallidae are known as dispersal vectors for some propagules not (yet) known to be dispersed by dabbling ducks, including several species of macroinvertebrates.

True variation between dispersal vectors, as found in the few studies that investigated multiple dispersal vectors simultaneously in a similar setup (see Charalambidou *et al.*, 2003), can probably be attributed to a combination of differences in diet and digestive physiology (e.g. Figuerola *et al.*, 2003; Green *et al.*, 2008). The diet and thereby qualitative dispersal of all bird species is likely to vary with season and food availability (Dessborn *et al.*, 2011). Seasonal and dietary effects on the dispersal of propagules have been included in some studies (see Figuerola *et al.*, 2003), but there were insufficient data for seasonality and dietary effects to be included in our meta-analysis.

Potential effects of bird physiology were addressed statistically. Despite the limited available data, we found quantitative dispersal to show a slight increase with increased body mass and to show a decrease with increased gizzard mass. Birds with higher body mass were also found to excrete a higher ratio of viable to non-viable propagules. The causes for this remain speculative. Although our calculations suggest higher numbers of propagules per dropping for larger bird species, birds that are much larger would typically also have a lower dropping rate (Hahn *et al.*, 2008) and smaller population sizes. Thus, other factors might reduce the number of propagules excreted over time by birds with higher body masses. Further experimental investigation is sorely needed to assess differences between bird species in similar circumstances (e.g. Charalambidou *et al.*, 2003). Preferably their digestive systems should be allowed to adjust to the diet of interest (Charalambidou *et al.*, 2005), and effects of fasting and timing of eating should be included (e.g. Figuerola & Green, 2005).

We found no differences in quantitative capacity to excrete propagules between bird species classified as predominantly herbivorous or omnivorous (feeding guild is indicated in Table 1 and Fig. 1a,b). Both guilds dispersed macroinvertebrates and plant seeds. Because assimilation efficiency of animal matter is usually higher than that of plant matter (Swanson & Bartonek, 1970; Castro *et al.*, 1989), it is plausible that birds classified as predominant herbivores deliberately forage on animal matter during the breeding season (Dessborn *et al.*, 2011). In addition, the abundance of macroinvertebrates on or around macrophytes or floating between accumulated seeds may promote accidental ingestion (Janzen, 1984). Consumed intentionally or not, both omnivorous and herbivorous birds are likely dispersal vectors for aquatic macroinvertebrates.

Propagule size

Propagule size has been put forward as an important adaptive trait for terrestrial (e.g. Traveset *et al.*, 2001) and aquatic propagules (e.g. DeVlaming & Proctor, 1968; Mueller &

Valk, 2002; Soons *et al.*, 2008; Wongsriphuek *et al.*, 2008). However, investigations into the effect of size on survival and retrieval of aquatic propagules have yielded contrasting results in past studies (Figuerola *et al.*, 2010) and rarely included macroinvertebrates. Our meta-analysis indicated that smaller propagules were retrieved in higher total percentages than larger propagules, confirming previous similar findings on plant seeds in mallards (Soons *et al.*, 2008). The available data suggested a propagule of 1 mm to have almost twice as much chance of being endozoochorously dispersed after ingestion than a propagule of 10 mm (Fig. 3). However, the low statistical power of this relationship, and lack of invertebrate studies, indicate that additional research is needed. In particular, experiments including larger sized propagules are required, as the effect of propagule size seems mainly driven by the lower retrieval of the larger propagules. This means that experiments interested in the effects of propagule size should make sure to include larger propagules (> 5 mm).

One of the additional challenges to such research will be to isolate the effect of propagule size from associated variation in morphological characteristics. The use of indigestible markers in feeding experiments (e.g. Charalambidou *et al.*, 2005; Figuerola & Green, 2005) may help eliminate the influence of morphological characteristics, although these also have limitations. Indigestible markers can be retained as grit or invoke a different response of the digestive system compared to digestible objects. Studies comparing effects of propagule size should preferably feed a mix of differently sized propagules to avoid different loading volumes of the digestive system when feeding equal numbers of differently sized propagules. The amount of propagules fed should be a trade-off between finding a low percentage of surviving organisms and overfeeding unrealistic large amounts of propagules resulting in regurgitation (Malone, 1965). As a guideline, successful previous studies fed on average 100–500 propagules with an average size of 3.5 mm per trial to birds the size of a mallard.

Smaller propagules were not only excreted in larger amounts, but they have also been shown to pass through the digestive system at a slower rate (Figuerola *et al.*, 2010), and are thus retained for longer periods. Because longer retention time will result in greater damage being inflicted (e.g. DeVlaming & Proctor, 1968; Afik & Karasov, 1995; Bauchinger *et al.*, 2009), a question for future studies will be whether smaller propagules escape digestion more easily or are more resistant to digestion. In conclusion, smaller propagules will have both highest survival and farthest dispersal by long retention, and will likely be produced and ingested in higher numbers in natural situations (Bruun & Poschlod, 2006; Brochet *et al.*, 2010).

Hypotheses on dispersal by birds that require further testing

The high frequency with which intact propagules can be found in bird droppings suggests that there is an underlying mechanism. First of all, propagule survival might be due to charac-

teristics of the propagules. Adaptations for gut passage have to date been found in certain plant seeds, whereby germination success actually increased after gut passage (e.g. Santamaría *et al.*, 2002; Wongsriphuek *et al.*, 2008). However, for many other surviving plant seeds and macroinvertebrates, no obvious adaptations have yet been identified. One might speculate that most species here identified to be capable of dispersal are merely adapted to survival in stochastic environments, for which they acquired adaptations that also provide suitability for dispersal by birds, rather than that they have special adaptations for dispersal by birds. Our overview of these taxa provides an ideal starting point for the identification of species characteristics or potential adaptations in propagules related to bird-mediated dispersal through phylogenetic analyses and analyses of species characteristics. Such an approach would facilitate exploration of the dispersal potential of species with similar characteristics, or even provide insight into evolutionary processes underlying bird-mediated dispersal.

A second potential explanation for the survival of propagules may be directly related to a digestive trade-off in the vector animals. Although the survival of propagules seems inefficient for foraging vectors because they effectively excrete undigested food, foraging birds achieve maximum net energy and nutrient gain over time at assimilation efficiencies (defined as the energy absorbed as a proportion of energy ingested, Castro *et al.*, 1989) lower than 100% assimilation efficiency. This is because increased assimilation efficiency necessitates increased retention time (e.g. Prop & Vulink, 1992) and therewith decreases total food intake over time, when food is abundant. In natural situations, the assimilation efficiency of a range of food types is therefore *c.* 75% in most birds (Castro *et al.*, 1989; Karasov & Levey, 1990). Assimilation efficiency can be further reduced when food intake rate increases (Kersten & Visser, 1996; Clauss *et al.*, 2007; van Gils *et al.*, 2008) or the bird's digestive system is atrophied in preparation for migration (e.g. McWilliams & Karasov, 2001). Often, part of all ingested food items will remain undigested, which provides a window of opportunity for propagules to be excreted intact. How digestive flexibility varies between bird species, within and between seasons, between food types and food availability, and during different activities such as flying and swimming, are interesting directions for future (experimental) research that will enhance our understanding of propagule dispersal.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 List of publications used.

Appendix S2 Explanation of the calculations for the quantitative dispersal model.

Appendix S3 Overview of propagules capable of bird-mediated dispersal.

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