Aquatic Botany 127 (2015) 1–5

Contents lists available at ScienceDirect

Aquatic Botany

journal homepage: www.elsevier.com/locate/aquabot

Short communication

Regurgitation by waterfowl: An overlooked mechanism for long-distance dispersal of wetland plant seeds

E. Kleyheeg[a,*], C.H.A. van Leeuwen[b,1]

[a] Ecology & Biodiversity group, Institute of Environmental Biology, Utrecht University, Padualaan 8, 3584CH Utrecht, The Netherlands
[b] Department of Aquatic Ecology, Netherlands Institute of Ecology, Droevendaalsesteeg 10, 6708 PB Wageningen, The Netherlands

ARTICLE INFO

Article history:
Received 11 November 2014
Received in revised form 25 June 2015
Accepted 30 June 2015
Available online 4 July 2015

Keywords:
Endozoochory
Long-distance seed dispersal
Macrophytes
Mallard (*Anas platyrhynchos*)
Riparian vegetation
Seed size
Waterbirds

ABSTRACT

Birds commonly regurgitate indigested particles after foraging. Many frugivorous birds regurgitate seeds ingested with the flesh of fruits, which importantly contributes to plant dispersal in terrestrial ecosystems. In freshwater ecosystems, waterbirds are known to defecate viable seeds in their faeces, but little is known about regurgitation as a potential additional seed dispersal mechanism. We experimentally fed eight mallards (*Anas platyrhynchos*) with a high and low volume of seeds of ten wetland plant species, and monitored regurgitation and defecation of intact seeds over 24 h. Regurgitation occurred at least once in all individual mallards and was induced by two different mechanisms: (i) feeding of high food volumes was significantly associated with regurgitation of all seed species from the crop after retention times of 1–3 h, and (ii) large indigestible seeds were expelled from the gizzard 11 or more hours after feeding. Seed regurgitation was much less plant species-specific than survival of seeds passing digestion, which suggests it is a particularly suitable dispersal mechanism for plant species unable to disperse by endozoochory (such as plant species with large, soft-bodied seeds). Observations of regurgitation by wild waterbirds are needed to improve our knowledge on this additional role of waterbirds in ecosystem functioning.

1. Introduction

Regurgitation, or vomiting, is a common behaviour in the daily life of many bird species. Deliberate regurgitation of food items has various functions for birds. Many seabirds use it for chick provisioning, as it enables them to carry prey over long distances to the nest (e.g., Wilson et al., 1989). Predatory birds foraging on vertebrates and insects regurgitate indigestible prey remains in pellets (e.g., Barrett et al., 2007; Tornberg and Reif, 2007). Many frugivorous birds swallow whole fruits, but digest only the fleshy parts (pulp) and regurgitate the seeds (Herrera, 1984; Foster, 1987; Jordano, 2000). This is thought to accelerate processing of nutritious pulp by avoiding passage of seeds through the entire digestive tract (Levey, 1987).

Interestingly, regurgitation might not only benefit the bird itself, but may also contribute to the life cycles of ingested organisms if these are regurgitated undamaged. Analogous to the mechanism of endozoochory by defecation of viable organisms after gut passage (reviewed by e.g., Herrera, 1984; Figuerola and Green, 2002; Van Leeuwen et al., 2012b), regurgitation may also contribute to long-distance dispersal. For terrestrial ecosystems, regurgitation is long known as an additional mechanism for seed dispersal (e.g., Jordano, 2000). In aquatic ecosystems, however, little attention has been paid to this potential dispersal mechanism.

To our knowledge, only few studies have focused on regurgitation of seeds by shorebirds (Proctor, 1968; Sanchez et al., 2005, 2006) and only one study specifically addressed regurgitation by waterfowl. Malone (1966) reported two instances of regurgitation during an experimental feeding trial with mallards (*Anas platyrhynchos*), which regurgitated loose pellets of *Chara* oospores about 45 min after feeding. Regurgitation by shorebirds was also observed to occur within one hour after feeding (DeVlaming, 1967). Both studies attributed regurgitation to overfeeding and gorging by the birds, but the short retention times suggested little importance for long-distance dispersal. Only one study so far reported regurgitation of large quantities of wetland plant seeds after long retention by shorebirds: Proctor (1968) retrieved regurgitated seeds until at least 100 h after ingestion by killdeer (*Charadrius vociferus*) and least sandpiper (*Calidris minutilla*). Regurgitation of intact propag-

* Corresponding author.
E-mail address: Kleyheeg@uu.nl (E. Kleyheeg).
[1] Present address: Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, Post Office Box 1066 Blindern, 0316 Oslo, Norway.

http://dx.doi.org/10.1016/j.aquabot.2015.06.009
0304-3770/

ules by shorebirds was only recently confirmed in field situations (Sanchez et al., 2005, 2006). Here, we specifically address the potential of regurgitation for dispersal of seeds by waterfowl, since Anatidae (ducks, geese and swans) are increasingly recognized as important vectors for seed dispersal, which is considered one of their main ecosystem services (Green and Elmberg, 2014).

Dabbling ducks in particular consume a wide range of seeds (Dessborn et al., 2011; M.B. Soons et al. unpublished data). Their digestive systems can efficiently digest most ingested materials, and relatively weak propagules (such as soft-bodied large seeds, fish eggs and many aquatic invertebrates) generally have a low probability of surviving passage through the entire digestive tract (Charalambidou et al., 2005; Van Leeuwen et al., 2012c). As endozoochory is often limited for this category of propagules, regurgitation might provide an alternative dispersal mechanism to explain wide distributions and rapid colonization of wetlands by species lacking the morphology for endozoochory. Dispersal by regurgitation circumvents many of the damaging digestive processes.

We hypothesize that regurgitation by waterfowl provides a suitable alternative dispersal mechanism for these species. During a series of feeding trials with captive mallards we encountered multiple occasions of seed regurgitation. This allowed us to specifically test the following hypotheses: (i) regurgitation by waterfowl is associated with overfeeding, (ii) regurgitation of seeds by Anatidae can occur even after long retention, and (iii) regurgitation is a particularly important dispersal mechanism for propagules which poorly survive passage through the entire digestive system (e.g., large, soft-bodied seeds).

2. Methods

2.1. Experimental set-up

In Aug–Sep 2011 we experimentally force-fed eight captive mallards with a known quantity of seeds and monitoring seed excretion by defecation and regurgitation over 24 h. For the initial purpose of the experiment (Kleyheeg et al., 2015), the mallards were exposed to five different activity treatments after feeding: sitting in a dry cage (0.54 × 0.46 × 0.48 m), floating on water without active swimming, and swimming at 0.2, 0.4 or 0.6 m s^{-1} in a flume tank (details in Van Leeuwen et al., 2012a). The wet treatments lasted six hours after which the mallards were placed in a dry cage for the remainder of the 24 h.

During all treatments, defecated and regurgitated seeds were collected every hour for the first 12 h, and once more after 24 h. The dry treatment cages were equipped with a tray beneath a mesh wire bottom, and seeds in the flume tank were collected in nylon filters (0.680 mm mesh). At the start of each trial, each individual mallard was fed with either a high-volume (first set of trials) or a low-volume (second set of trials) mixture of seeds.

For the high-volume trials, the mallards were fed with differently sized seeds of 10 wetland plant species varying in volume between 0.3 and 140.0 mm^3 (for details per species see Fig. 1). Each mallard was fed 100 seeds per plant species from seven species with relatively small seeds (*Althaea officinalis*, *Carex riparia*, *Lotus pedunculatus*, *Lycopus europaeus*, *Persicaria bisorta*, *Sanguisorba officinalis* and *Thalictrum flavum*) and 50 seeds from three larger-seeded species (*Agrostemma githago*, *Impatiens glandulifera* and *Iris pseudacorus*). This resulted in a total ingested volume of 10.1 cm^3. For the low-volume trials we fed each mallard an identical seed mixture, however, now excluded the seeds of *I. pseudacorus* (the species with the largest seeds). The combined volume of this mixture was 3.1 cm^3. Seeds were administered in dough pellets, hence a thin layer of dough was added to the volume in both treatments. Similar

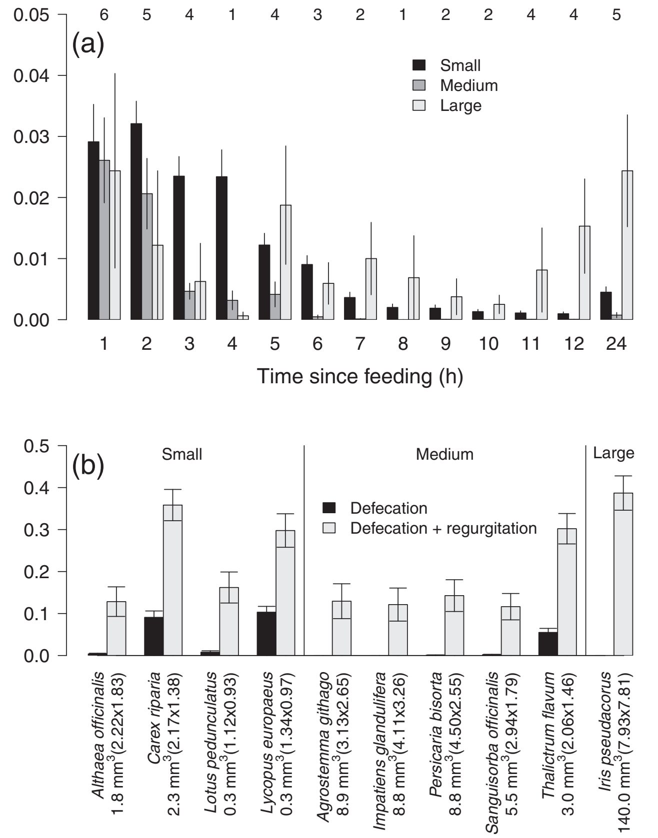

Fig. 1. (a) Retrieval pattern over time of excreted seeds (expressed as a proportion of the number of ingested seeds) in three size classes in all trials where regurgitation occurred. Small seeds include species <5 mm^3, medium is 5–10 mm^3, and large is >10 mm^3. Numbers above columns indicate number of observed regurgitation events during that hour. (b) Mean proportion of intact seeds retrieved for each species in trials with and without regurgitation. For all species, the trials with regurgitation resulted in a higher proportion of retrieved seeds (statistics in Table 1). Species specific means of seed volume (in mm^3), length and width (in mm) are indicated on the horizontal axis.

methods were applied successfully in previous experiments without reports of regurgitation (Charalambidou and Santamaría, 2002; Santamaría et al., 2002; Charalambidou et al., 2005; Van Leeuwen et al., 2012a). In the high-volume trials, all eight mallards participated in the dry cage treatment, but they were randomly subjected to the four remaining treatments, so that all individual mallards received two wet treatments (in total 24 high-volume trials). In the low-volume experiment, all mallards received all five treatments (in total 40 low-volume trials). Regurgitation was detected by continuous observation of the mallards for the first 12 h or by the presence of regurgitated dough pellets.

2.2. Data analysis

Regurgitation events were readily detected, but we were unable to fully separate regurgitated from defecated seeds as they mixed up on the tray or in the nylon filters. To avoid possible biases by wrong categorization of seeds, we used the total number of excreted intact seeds per species per collection moment in the statistical analyses (i.e., the sum of regurgitated and defecated seeds for the hours in which regurgitation had occurred). All results were analysed in two generalized linear mixed-effects models.

In a first model (model I), whether or not an individual bird regurgitated (yes/no) was the binomial dependent variable with logit link function, depending on activity level and the volume of seeds fed (high/low) as fixed factors. Individual bird ID was included as random factor to correct for repeated measures within individuals. In a second model (model II), the proportion of ingested seeds that was retrieved after 24 h was the binomial denominator variable depending on whether or not a bird had regurgitated (yes/no) and plant species (10 levels) as fixed factors. To detect whether or not birds that regurgitated excreted a higher proportion of seeds for particular plant species only, we also included the interaction between plant species and the occurrence of regurgitation, and used Tukeyís post-hoc comparisons to detect for which plant species regurgitation resulted in higher overall retrieval. Activity level and individual bird ID were included in this model as random factors.

Model selection started with the full models from which factors were stepwise removed. If removal of a term increased the AICc value (for small sample sizes) by more than 2.0 we assumed it to contribute significantly to the model (Burnham and Anderson, 2002). All calculations were performed using R for statistics (R Development Core Team, 2015). The generalized mixed models were compared using Maximum Likelihood estimations in package "lme4"; the posthoc test were performed with package "multcomp".

3. Results

Regurgitation occurred in 29 of the 64 feeding trials, at least once in all individual mallards. Most regurgitation was observed in the first 3 h (35% of all cases of regurgitation) and after 10 h (30%, Fig. 1a). Total feeding volume strongly affected the frequency of regurgitation, as it occurred in 12.5% of the low-volume trials, versus 91.7% of the high-volume trials (Model I: $Z = 4.84$, $p < 0.001$, Table 1). Activity treatment did not affect the regurgitation frequency ($Z = -1.00$, $p = 0.32$, Table 1). For all seed species the mean number of retrieved intact seeds was higher during trials in which regurgitation had occurred (Model II: overall $Z > 8.88$, $p < 0.01$, Fig. 1b). The seed excretion pattern over time showed that regurgitation could occur after long retention in the digestive tract (Fig. 1a, regurgitation after >10 h was observed in 6 out of 8 mallards).

When considering only trials in which regurgitation had occurred, we observed distinct patterns for three different size classes of ingested seed species. The retrieval of the smallest seeds (<3 mm^3) was high during the first hours and gradually decreased only after four hours, reflecting relatively frequent passage through the digestive tract, additional to regurgitation early after ingestion. Medium-sized seeds (3–10 mm^3) survived gut passage poorly and were mainly retrieved in the first 2 h after feeding. This early regurgitation often involved complete pellets or parts of pellets with undamaged seeds, suggesting regurgitation from the crop rather than from the gizzard. The largest seeds (>10 mm^3) were retrieved exclusively in hours when regurgitation was observed. Their retrieval showed an irregular pattern during the first hours after ingestion, but clearly peaked after 11 h. These seeds were regurgitated long after ingestion and were found separate from faeces with damaged or missing seed coats; this indicates regurgitation from the gizzard.

4. Discussion

Regurgitation of ten wetland plant seeds by mallards was observed frequently after feeding in an experimental setup. During the first hours after feeding, regurgitation occurred mainly as a response to feeding large volumes. However, large, tough seeds were also frequently regurgitated after long retention (>10 h). This indicates that regurgitation by waterfowl has a significant potential as long-distance seed dispersal mechanism. Analogous to seed dispersal by frugivorous birds in terrestrial systems (Herrera, 1984), regurgitation by waterfowl could be an additional, largely overlooked, dispersal mechanism for aquatic propagules.

4.1. Feeding volume and seed size

The frequency of regurgitation showed a bimodal pattern over time, suggesting two different mechanisms for regurgitation. Regurgitation relatively shortly after feeding was observed primarily in mallards fed with a high volume and generally involved regurgitation of complete feeding pellets. The strong association of regurgitation with feeding volume indicates that early regurgitation is a response to overfeeding, as suggested previously (Malone, 1966; Stewart, 1967; DeVlaming, 1967; Jordano, 2000). Small and medium sized seeds that were not regurgitated were either digested or defecated, and only rarely regurgitated after longer retention.

In contrast, large seeds (*I. pseudacorus* in this study) showed a second regurgitation peak 10–12 h after feeding in six out of eight mallards. This was long after most of the smaller seeds had been digested or defecated, and is therefore unlikely related to overfeeding. The regurgitated large seeds had damaged seed coats, indicating retention in the gizzard at least part of the time. Regurgitation after long retention might be explained by the size of the entrance of the duodenum (maximum stretched circumference ca. 23 mm, $N = 10$, unpublished data by E.K.), which food particles have to pass to enter the small intestines after processing in the gizzard. If large seeds are not broken down in the gizzard and cannot enter the small intestines, expelling these seeds may allow more efficient processing of other food items. This second mechanism would be analogous to the rejection of seeds in fruits that are larger than the gape width of frugivorous birds (Wheelwright, 1985).

4.2. Regurgitation versus defecation

Regurgitation increased seed retrieval for all plant species in this study, but most notably for species that were unable to resist digestion. Seeds of *A. githago* and *I. glandulifera* were never retrieved from faeces, but were retrieved intact and able to germinate after regurgitation (pers. obs. E.K.). While plant species typically show high variation in their ability to resist complete digestion (Soons et al., 2008), such interspecific variability was not observed for regurgitation. Regurgitation after short retention times as a response to feeding on large volumes is a non-selective dispersal mechanism possible for all ingested plant seeds, and can therefore provide a particularly suitable dispersal mechanism for soft-bodied propagules. Even if regurgitation occurs only a few hours after ingestion, this could already facilitate dispersal of less-resistant plant seeds and organisms like fish eggs and macro- invertebrates towards new habitats.

The regurgitation observed after long retention times was related to feeding on large seeds. These large seeds generally do not survive passage through the complete digestive system for dispersal by defecation very well (Van Leeuwen et al., 2012b). For these large-seeded species, we suggest that regurgitation is a highly effective alternative long-distance dispersal mechanism. Regurgitation after long retention is more species-specific and particularly facilitates dispersal of large, tough seeds.

4.3. Regurgitation in the field

The regurgitation we observed during our experiment followed feeding birds with a large volume of seeds in a short period of time, and included feeding large seeds. The crucial question is whether or not this will also occur in natural situations, as still little is known about regurgitation in free-ranging mallards and

Table 1
Results from the two generalized mixed models. **Δ**AICc values indicate changes in AICc due to removal of each term. Bold terms remained in the final best model. High volume was set as the intercept for factor volume fed in Model I; and "no regurgitation" as the intercept for factor regurgitation in Model II.

Model	Dependent variable	Variance explained by random factor		Explanatory predictor variable	Df	Estimate	SE	Z-value	*P*-value	ΔAICc
I	Regurgitation (1/0)	Bird ID	0.00	**Intercept**		−1.43	0.66	−2.15	0.03	
				Volume fed	1	4.39	0.91	4.85	<0.001	Δ +40.2
				Activity level	1	−0.29	0.29	−1.00	0.32	Δ +1.2
II	Proportion retrieved seeds	Bird ID	0.069	**Intercept**		−19.67	431.1	-0.046	0.964	
		Activity level	0.092	**Regurgitated (yes/no)**	1	1.93	0.04	49.15	<0.001	
				Plant species	9					
				Regurgitated (yes/no) × plant species	9					Δ +555.4
				Agrostemma githago		Only seeds retrieved by regurgitation				
				Althaea officinalis		3.58	0.28	12.62	<0.01	
				Carex riparia		1.47	0.07	20.78	<0.01	
				Impatiens glandulifera		Only seeds retrieved by regurgitation				
				Iris pseudacorus		Only seeds retrieved by regurgitation				
				Lotus pedunculatus		3.09	0.20	15.46	<0.01	
				Lycopus europaeus		1.14	0.07	16.55	<0.01	
				Persicaria bisorta		5.15	0.58	8.88	<0.01	
				Sanguisorba officinalis		4.10	0.38	10.72	<0.01	
				Thalictrum flavum		1.78	0.09	20.93	<0.01	

other dabbling ducks. Mallards are known as highly opportunistic foragers (Dessborn et al., 2011) and often gorge themselves with suddenly available food in their habitat, up to the maximum capacity of their crop (Stewart, 1967). Large food items such as acorns can make up significant parts of their opportunistic diet (Combs and Fredrickson 1996). Gorging behaviour is commonly induced by strong spatiotemporal variation in food availability (to take advantage of high local food abundance), combined with a time budget trade-off between foraging and vigilance (Guillemain et al., 2002). Although our experiments involved force-feeding, the food intake rate was not necessarily very different from natural conditions. Malone (1966) and Stewart (1967) described regurgitation events after birds fed voluntarily until their crops were completely full. Stewart (1967) proposed that regurgitation after foraging could be necessary when seeds in the crop swell by taking up water, thus explaining how voluntary overfeeding can subsequently lead to excessive food volumes in the digestive system.

Large, tough seeds such as those of *I. pseudacorus* occur in the natural diet of mallards (M.B. Soons et al., unpublished data), but rarely pass the digestive tract in feeding trials (Soons et al., 2008; Kleyheeg et al., 2015). Our observations show that large, indigestible seeds may be regurgitated after long retention times, unrelated to overfeeding, which may also be the mechanism for expelling large grit particles. As regurgitation in birds requires a suffocate movement which is impossible during flight (Breitbach et al., 2012), regurgitation most likely occurs after landing in wetland habitat, making it an even more directed dispersal mechanism for aquatic organisms than defecation.

4.4. Conclusion

Regurgitation by mallards within several hours after feeding seems a common response to overfeeding, and may be an important, yet largely overlooked dispersal mechanism for aquatic organisms. Regurgitated after long retention (>10 h) mostly occurred for large, tough seeds, probably because they were too large to efficiently pass the digestive tract and too tough to be grinded by the gizzard. Regurgitation shortly after ingestion was unrelated to seed traits, providing an especially important mechanism for the dispersal of large and soft-bodied seeds (or other propagules found in Anatidae diets), which are unable to benefit from dispersal by defecation. More observations of regurgitation by waterfowl under natural conditions are needed to enhance our understanding of this dispersal mechanism.

Acknowledgements

We thank Mary Ann Morison, Peter de Vries and Bart van Lith for practical assistance and Bart Nolet and Merel Soons for contributions to the study design. We thank two anonymous reviewers for their valuable comments on a previous version of this manuscript. The experiment has been carried out at the Netherlands Institute of Ecology (publication number 5891) under license number NIOO11.05 of the KNAW Animal Experiments Committee. This research was funded by the Netherlands Organization for Scientific Research (NWO-ALW; VIDI grant 864.10.006 to Merel B. Soons).

References

Barrett, R.T., Camphuysen, K., Anker-Nilssen, T., Chardine, J.W., Furness, R.W., Garthe, S., Hüppop, O., Leopold, M.F., Montevecchi, W.A., Veit, R.R., 2007. Diet studies of seabirds: a review and recommendations. ICES J. Mar. Sci 64, 1675–1691.
Breitbach, N., Böhning-Gaese, K., Laube, I., Schleuning, M., 2012. Short seed-dispersal distances and low seedling recruitment in farmland populations of bird-dispersed cherry trees. J. Ecol., 1349–1358.
Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: a Practical Information-theoretic Approach. Springer, New York.
Charalambidou, I., Santamaría, L., 2002. Waterbirds as endozoochorous dispersers of aquatic organisms: a review of experimental evidence. Acta Oecol. 23, 165–176.
Charalambidou, I., Santamaría, L., Jansen, C., Nolet, B.A., 2005. Digestive plasticity in mallard ducks modulates dispersal probabilities of aquatic plants and crustaceans. Funct. Ecol. 19, 513–519.
Combs, D.L., Fredrickson, L.H., 1996. Foods used by male Mallards wintering in Southeastern Missouri. J. Wildl. Manage. 60, 603–610.
Dessborn, L., Brochet, A.L., Elmberg, J., Legagneux, P., Gauthier-Clerc, M., Guillemain, M., 2011. Geographical and temporal patterns in the diet of pintail Anas acuta, wigeon Anas penelope, mallard Anas platyrhynchos and teal Anas crecca in the Western Palearctic. Eur. J. Wildl. Res. 57, 1119–1129.
DeVlaming, V.L., 1967. Regurgitation by killdeer as a possible means of dispersal for seeds and aquatic organisms. Wilson Bull. 79, 449–450.
Figuerola, J., Green, A.J., 2002. Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. Freshw. Biol 47, 483–494.
Foster, M.S., 1987. Feeding methods and efficiencies of selected frugivorous birds. Condor 89, 566–580.
Green, A.J., Elmberg, J., 2014. Ecosystem services provided by waterbirds. Biol. Rev. 89, 105–122.
Guillemain, M., Martin, G.R., Fritz, H., 2002. Feeding methods, visual fields and vigilance in dabbling ducks (Anatidae). Funct. Ecol 16, 522–529.
Herrera, C.M., 1984. Adaptation to frugivory of Mediterranean avian seed dispersers. Ecology 65, 609–617.
Jordano, P., 2000. Fruits and frugivory. In: Fenner, M. (Ed.), Seeds: The Ecology of Regeneration in Plant Communities. Cabi publishers, Wallingford, UK, pp. 125–166.
Kleyheeg, E., van Leeuwen, C.H.A., Morison, M.A., Nolet, B.A., Soons, M.B., 2015. Bird-mediated seed dispersal: reduced digestive efficiency in active birds modulates dispersal capacity of plant seeds. Oikos (online early, DOI: 10.1111/oik.01894).

Levey, D.J., 1987. Seed size and fruit-handling techniques of avian frugivores. Am. Nat. 129, 471–485.
Malone, C.R., 1966. Regurgitation of food by Mallard ducks. Wilson Bull. 78, 227–228.
Proctor, V.W., 1968. Long-distance dispersal of seeds by retention in digestive tract of birds. Science 160, 321–322.
R-Development-Core-Team, 2015. R. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL: http://www.R-project.org
Sanchez, M.I., Green, A.J., Castellanos, E.M., 2005. Seasonal variation in the diet of Redshank Tringa totanus in the Odiel Marshes, southwest Spain: a comparison of faecal and pellet analysis. Bird Study 52, 210–216.
Sanchez, M.I., Green, A.J., Castellanos, E.M., 2006. Internal transport of seeds by migratory waders in the Odiel marshes, south-west Spain: consequences for long-distance dispersal. J. Avian Biol. 37, 201–206.
Santamaría, L., Charalambidou, I., Figuerola, J., Green, A.J., 2002. Effect of passage through duck gut on germination of fennel pondweed seeds. Arch. Hydrobiol. 156, 11–22.
Soons, M.B., Van der Vlugt, C., Van Lith, B., Heil, G.W., Klaassen, M., 2008. Small seed size increases the potential for dispersal of wetland plants by ducks. J. Ecol. 96, 619–627.
Stewart, P.A., 1967. Disgorging of food by Wood ducks. Wilson Bull. 79, 339.
Tornberg, R., Reif, V., 2007. Assessing the diet of birds of prey: a comparison of prey items found in nests and images. Ornis Fenn. 84, 21–31.
Van Leeuwen, C.H.A., Tollenaar, M.L., Klaassen, M., 2012a. Vector activity and propagule size affect dispersal potential by vertebrates. Oecologia 170, 101–109.
Van Leeuwen, C.H.A., Van der Velde, G., Van Groenendael, J.M., Klaassen, M., 2012b. Gut travellers: internal dispersal of aquatic organisms by waterfowl. J. Biogeogr. 39, 2031–2040.
Van Leeuwen, C.H.A., Van der Velde, G., Van Lith, B., Klaassen, M., 2012c. Experimental quantification of long distance dispersal potential of aquatic snails in the gut of migratory birds. PLoS One 7, e32292.
Wheelwright, N.T., 1985. Fruit size, gape width, and the diets of fruit-eating birds. Ecology 66, 808–818.
Wilson, R.P., Ryan, P.G., Wilson, M.P., 1989. Sharing food in the stomachs of seabirds between adults and chicks – a case for delayed gastric-emptying. Comp. Biochem. Physiol. A Comp. Physiol. 94, 461–466.