Aquatic Invasions 2025 Volume 20, Issue 4: 451–460

Research Article

Experimental evidence of internal transport of invasive apple snail eggs by waterbirds

Yang Zhao[1,2], Qichen Zhang[1], Andy J. Green[2], Sixian Tang[1], Xiaodong Jiang[1]

1 School of Life Sciences, East China Normal University, Shanghai, China

2 Department of Conservation Biology and Global Change, Estación Biológica de Doñana, EBD-CSIC, Américo Vespucio 26, Sevilla, Spain

Corresponding author: Xiaodong Jiang (xdjiang@bio.ecnu.edu.cn)

Abstract

The potential role of waterbirds in the dispersal of invasive apple snail *Pomacea canaliculata* was evaluated by feeding their eggs to mallards *Anas platyrhynchos* and quantifying the recovery of intact and viable eggs in their faeces and regurgitations. A total of 30,400 eggs were ingested by eight male mallards in 19 feeding trials. Endozoochory potential was detected in 14 trials, in which a total of 46 intact eggs were recovered from mallard faeces, and 684 intact eggs were regurgitated. Most intact snail eggs in faeces were egested 2–6 hours after feeding (72%), whereas 81% of those regurgitated were egested less than 1 hour after feeding. Two snail eggs from faeces and 74 eggs from regurgitations were successfully hatched (jointly representing 0.25% of ingested eggs). These data suggest that apple snail eggs can survive gut passage by waterbirds, and long-distance endozoochory events may contribute to the spread of the snail in the introduced range. In addition, short-distance dispersal is crucial and should not be overlooked as a means to sustain population, increase the extent of invaded range, and maintain gene flow.

Key words: Dispersal, biological invasion, apple snail, waterbirds, endozoochory

Academic editor: Mikhail Son
Received: 15 December 2024
Accepted: 26 May 2025
Published: 12 November 2025

Citation: Zhao Y, Zhang Q, Green AJ, Tang S, Jiang X (2025) Experimental evidence of internal transport of invasive apple snail eggs by waterbirds. Aquatic Invasions 20(4): 451–460. https://doi.org/10.3391/ai.2025.20.4.175069

Copyright: © Yang Zhao et al.
This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

Introduction

Biological invasions are one of the main causes of biodiversity loss and species extinctions, second only to habitat loss (Bellard et al. 2016). As research progresses, more interactions related to biological invasions are being discovered, providing new insights into global changes. These include interactions between native and invasive species, and among invasive species themselves (Bertolero et al. 2022; Lovas-Kiss et al. 2023; Céspedes et al. 2024). Fundamentally, biological invasions are driven by dispersal, which promotes the spread of organisms at the landscape scale (Reynolds et al. 2015). However, successful invasions also depend on post-dispersal processes, like establishment in new habitats and persistence through biotic interactions and meta-community dynamics, sustained by propagule pressure and repeated dispersal events (Hufbauer et al. 2013; Wu et al. 2023). Alien species are often particularly effective at dispersing, leading to widespread global distribution of certain invasive species (Green 2016).

Freshwater ecosystems provide vital ecosystem services and harbor exceptional biodiversity, yet face disproportionate invasion impacts (Reynolds et al. 2015; Green 2016). Global freshwater systems host hundreds of invasive species—including *Eichhornia crassipes*, *Ludwigia grandiflora*, *Spartina densiflora*, cyprinid fishes and crayfish—with documented ecological disruptions (García-Alvarez et al. 2015; Lovas-Kiss et al. 2018; Lovas-Kiss et al. 2020). Among these invaders, South American apple snails *Pomacea canaliculata*-complex exemplify severe invasion consequences (Global Invasive Species Database 2024). This thermophilic species invades rice ecosystems globally, from Asian paddies to North American littoral zones (Liu et al. 2018), while establishing European populations as novel prey for glossy ibis *Plegadis falcinellus* and yellow-legged gull *Larus michahellis* (Bertolero and Navarro 2018; Bertolero et al. 2022). They are known to damage rice seedlings and other crops, and they feed on submerged plants, impacting nutrient cycling in ponds and streams, altering plant community composition, and subsequently affecting the diversity of zooplankton (Horgan et al. 2014). Rapid maturation (4 months) and high fecundity (thousands of eggs in life), coupled with genetic diversity (Estebenet and Martin 2002), drive their expansion. They lay eggs above the waterline, on stems and leaves of aquatic plants, as well as deposit eggs on human structures like bridges and docks. Eggs deposited on aquatic vegetation and human infrastructure are toxin-protected and considered to be unpalatable for amphibians (Brola et al. 2021), though waterbirds partially suppress populations through predation (Liang et al. 2013). Notably, in Florida, invasive apple snails *P. maculate* compete with native *P. paludosa*, and local snail kites have increasingly consumed the more-abundant invasive snails, despite their larger and thicker shells (Machado-Stredel et al. 2024).

While migratory birds are key vectors of long-distance dispersal, short-distance dispersal via repeated stepping-stone events proves equally vital for biological invasions (Coughlan et al. 2017a). Zebra mussel *Dreissena polymorpha* and *Lemna minuta* could frequently be transported over short distance, with mallards *Anas platyrhynchos* acting as typical vectors (Coughlan et al. 2017b, 2017c). Field evidence reveals the role of waterbirds as invasion vectors: gulls and storks disperse alien plant seeds and invertebrates through defecation and regurgitation (Lovas-Kiss et al. 2018; Martín-Vélez et al. 2021), while shorebirds transfer the cysts of North American brine shrimp *Artemia franciscana* to European wetlands (Green et al. 2005). Crucially, invasive snails can survive avian gut passage (Martín-Vélez et al. 2021), demonstrating waterbirds' capacity to carry snails across geographical barriers. Despite these documented mechanisms, waterbird-mediated dispersal remains understudied in invasion ecology (Green et al. 2023; Lovas-Kiss et al. 2023). Effective invasive species management requires integrating zoochory mechanisms into control strategies; however, current approaches frequently neglect these pathways (Green 2016; Reynolds et al. 2017).

To investigate the role of waterbirds in endozoochory, researchers have conducted various feeding experiments. In one study, mallards were fed to seeds from congeneric native and invasive plant species, revealing that avian ingestion delays invasive plant germination (Lovas-Kiss et al. 2023). Another experiment demonstrated that mallards disperse fragile invasive cyprinid eggs via defecation, with a subset resisting digestion (Lovas-Kiss et al. 2020). Beyond defecation, ducks can regurgitate propagules under specific conditions. For instance, mallards expel large indigestible seeds from the gizzard up to 10 hours after ingestion (Kleyheeg and van Leeuwen 2015). Regurgitation may be crucial for invertebrates or their propagules that are unable to survive passage through the intestines.

The aim of our study was to experimentally investigate whether waterbirds can facilitate the dispersal of apple snails *Pomacea canaliculata* by dispersing their eggs

through endozoochory. We hypothesized that a fraction of snail eggs would survive passage through mallard guts and be egested in faeces in a viable state. In addition, we expected that a portion of eggs fed to mallards might later be regurgitated and have a higher hatchability than those retrieved from faeces. We discussed the implications of our findings for the spread, impact, and potential control of alien apple snails.

Methods

Mallards *Anas platyrhynchos* are omnivorous birds that are widespread, numerous and highly mobile, serving as vectors for many plants and aquatic invertebrates (Urgyán et al. 2022; Green et al. 2023). Eight six-month-old male mallards were purchased from a poultry farm in Zhejiang Province. In China, some farmers cultivate apple snails *Pomacea canaliculata* for human consumption. During the apple snail breeding season, farmers sell surplus eggs so that others can rear snails. Consequently, obtaining apple snail eggs from farmers was straightforward. First, we offered a mixture of rice and apple snail eggs as food to the mallards, and confirmed that they fed on the eggs, even when other food was available (Suppl. material 1). This suggests that waterbirds are likely to ingest snail eggs in the wild, and we further investigated their ability to act as dispersal vectors for snail eggs using a controlled experiment.

During the experiment, mallards were kept individually in metal cages (0.40 × 0.40 × 0.60 m) with a mesh floor (2 × 15 cm), and removable plastic trays were placed under each cage to collect droppings. The apple snail eggs we purchased were attached to the stems of aquatic plants. After carefully removing the eggs from the stems, they were separated one by one and counted. This process caused some egg damage, and only the intact eggs were used for feeding and hatching experiments. Separated snail eggs are approximately 2 mm in diameter, and were placed in edible capsules and force-fed to mallards (Fig. 1). The capsules were purchased online from Gaohua Pharmaceutical. Each capsule had a cross section diameter of 8 mm and a length of 22 mm, and was made with glutinous rice flour. At 41 °C, the internal temperature of mallards (Tesson et al. 2018), we confirmed that capsule completely dissolves in water within 10 min when stirred slightly. The capsule may have protected the eggs to some extent, particularly by preventing the mallards' chewing process and partially withstanding physical and chemical digestion, which may have increased our recovery rate.

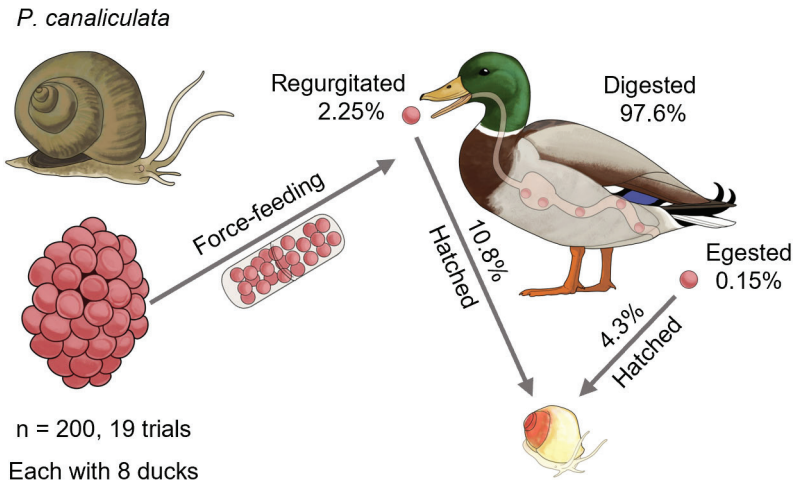

Figure 1. The number of apple snail eggs fed, with proportions of intact eggs regurgitated and defecated, and of juvenile snails that hatched following internal transport.

A total of 19 feeding trials were conducted over three months. In each trial, all eight mallards were fed 200 eggs separately. The feeding trials were numbered 1 to 19 in chronological order, and each individual mallard was force-fed a total of 3,800 apple snail eggs during the whole experiment. Faeces and regurgitation pellets were collected from the removable trays at 1, 2, 4, 6 and 8 h intervals after force-feeding, and then were immediately filtered through a sieve with a mesh size of 800 μm under tap water to recover intact eggs. Regurgitated and defecated eggs were easily distinguished, the latter being covered in faeces (Fig. 2).

Recovered intact eggs were immediately placed in plastic petri dishes in a hatching chamber at high humidity, a temperature of 25 °C, and 24-hour light for 30 days incubation. In each trial, 150 additional snail eggs from the same

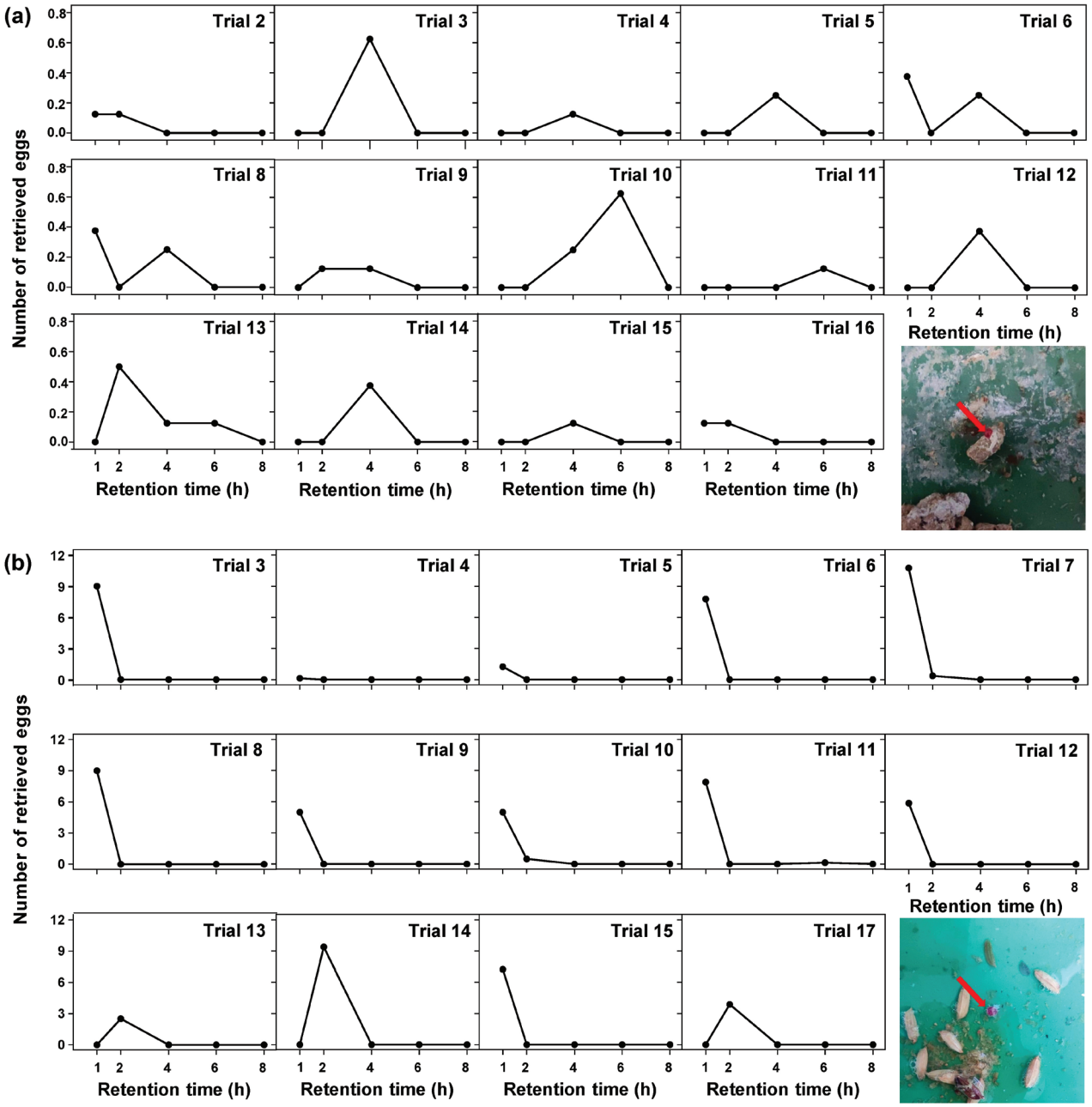

Figure 2. Retention time for intact eggs of apple snails recovered from (a) faeces and (b) regurgitated pellets of eight male mallards in 19 feeding trials. Data represent the means values for individual birds. Trials in which no egg was recovered in egesta are excluded from the figure. The images show intact eggs within faeces and regurgitated pellets.

batch, not fed to ducks, were divided equally into three control groups, and incubated under the same conditions.

Trials were separated by intervals of 1 to 15 days. Water and whole grain rice were available to the mallards ad libitum throughout the experiment. The ducks did not exhibit any obvious ill effects during the experiment. At the end of the study, the ducks remained in good health and were retained in captivity. The experiment was approved by the laboratory animal welfare and ethics committee of East China Normal University (No. q20240102).

Statistical analyses

Given the high proportion of zeros and lack of normality in our data, we used non-parametric statistics to compare the eggs recovery, retention time, and hatchability. For all trials, the Chi-square test was applied to analyze the frequency of defecation and regurgitation events. In order to control for potential variation among feeding trials, we selected all 12 trials in which eggs were recovered in both manners. Wilcoxon signed-rank test was used to compare the number of defecated and regurgitated eggs from the same trial in pairs. Then, we analyzed retention time of the eggs recovered from faeces and pellets using Mann-Whitney U test. Finally, we compared the hatchability of those eggs retrieved from faeces, pellets and the control in pairs, excluding trials in which no egg was recovered. In general, the sample size varied according to the number of trials with both kinds of eggs, except for the frequency analysis of defecation and regurgitation events.

Results

A total of 30,400 apple snail eggs were fed to eight male mallards in 19 feeding trials. In five feeding trials, no egg was recovered from faeces, while 4–6 intact eggs (ca. 0.15% of those ingested, Fig. 1) were recovered from faeces in the remaining 14 trials. Most eggs recovered from faeces were collected between 2 and 6 hours after feeding (Fig. 2). Regurgitation events were observed within 2 h after force-feeding (Fig. 2). In five feeding trials, no egg was regurgitated, while 684 intact eggs (ca. 2.25%, Fig. 1) were recovered in the remaining feeding trials. In the first hour 551 eggs were regurgitated, followed by 133 eggs in the second hour. The frequency of defecation events was higher than that of regurgitation events, but there was no significant difference in their occurrence (Chi-square test, $\chi^2 = 1.06$, $P = 0.3$). For a given trial, there was also no significant difference in the number of eggs defecated and regurgitated (Wilcoxon signed-rank test, N = 12 trials, $P = 0.15$), despite the latter being greater in quantity. The retention time of defecated eggs (3.68 ± 1.33 hours, Mean ± SD, N = 14 trials) and that of regurgitated eggs (1.22 ± 0.42 hours, Mean ± SD, N = 14 trials) was significantly different (Mann-Whitney U test, $P < 0.001$).

The incubation period for eggs that hatched varied from 5 to 15 days. Egested eggs generally showed lower hatchability than control eggs that had not been ingested. Control egg hatchability ranged from 26% to 94.7% (Fig. 3). Two intact eggs recovered from faeces in the 13th and 14th trial hatched successfully. The overall hatching rate of snail eggs from mallard faeces was 4.3% (Fig. 1), and the hatching rate of snail eggs from regurgitations was 10.8% (74 eggs from nine trials were hatched). Mann-Whitney U test showed that control eggs had a significantly higher hatchability than eggs from faeces (N = 14 trials, $P < 0.001$) and regurgitations (N = 14 trials, $P < 0.001$). Regurgitated eggs also had a significantly higher hatchability than eggs from faeces ($P = 0.02$). Overall, 0.007% of ingested eggs hatched after being egested in faeces, and a further 0.243% hatched after being regurgitated (Fig. 1).

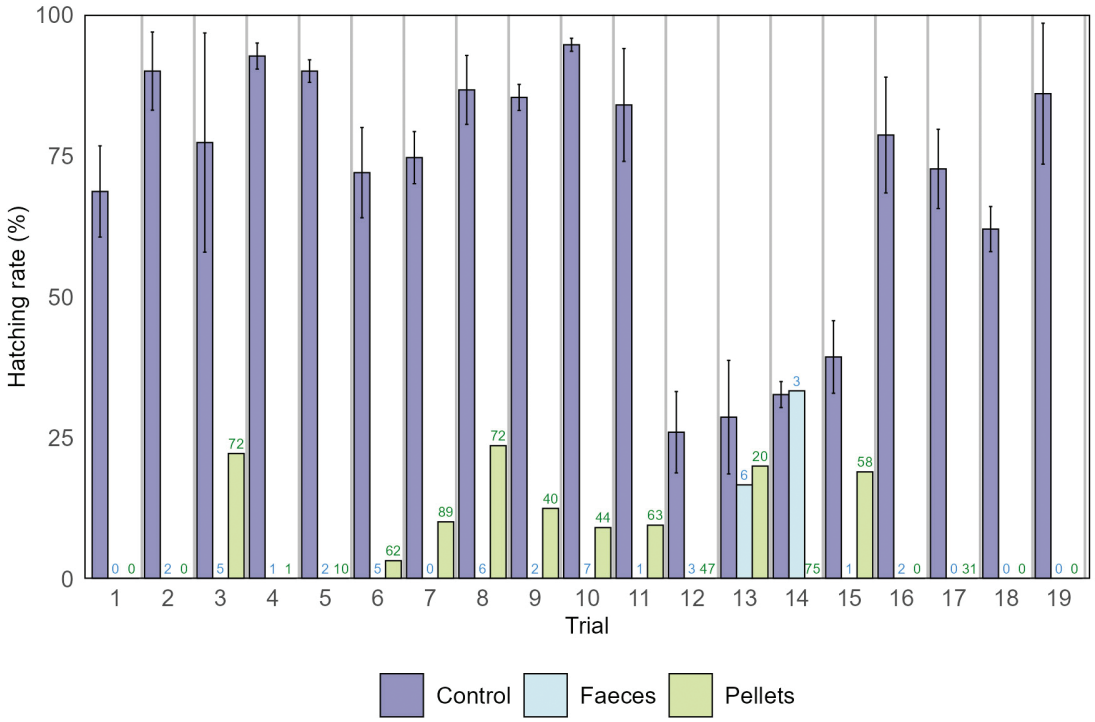

Figure 3. Hatching rate of apple snail eggs, comparing control eggs with those retrieved from faeces and regurgitated pellets for eight male mallards in 19 feeding trials. Numbers above the bars indicate the number of eggs recovered in each trial. The number 0 indicates no egg was recovered from faeces or pellets in this trial. All controls began with 150 eggs, divided equally into three groups.

Discussion

Our study provides the first experimental evidence of waterbird-mediated dispersal for invasive apple snail eggs. Crucially, regurgitation enables short-distance dispersal, while intestinal retention facilitates long-range dispersal. This mechanism complements human-mediated dispersal, explaining their rapid colonization of global wetlands within decades. In southern China, waterbird predation may partially suppress their populations (Liang et al. 2013), yet dispersal persists: their eggs can remain in mallard guts for up to 6 hours, and viable eggs could potentially be transported more than 400 km at flight speeds of 60–78 km·h^{-1} (Reynolds et al. 2015). Given their body size, adults cannot be dispersed by surviving gut passage in a manner comparable to the alien *Physella acuta* (Martín-Vélez et al. 2021). Our study showed that the dispersal of apple snail eggs is rare but possible, since mallards actively ingest them and a small but important fraction can survive gut passage. The same may be true for other waterbird species, such as Anatidae, storks and gulls, occurring in rice fields and other habitats invaded by apple snails (Martín-Vélez et al. 2021).

Laboratory and field studies have conclusively demonstrated that waterbirds can disperse a wide range of animal taxa by endozoochory, including chironomid larvae, aquatic beetle eggs, and fish eggs (Green and Sanchez 2006; Laux and Kölsch 2014; Lovas-Kiss et al. 2020). This ecological context supports our finding that apple snail eggs can survive avian gut passage. While regurgitation and defecation both contribute to dispersal (Kleyheeg and van Leeuwen 2015), regurgitation specifically enables short-distance transport of larger quantities of eggs, whereas defecation facilitates long-distance movement of fewer propagules. Such dynamics mirror stepping-stone dispersal, where sequential short-distance movements bridge distant habitats and may transform these localized events into landscape-scale invasions over time, as observed in bivalves spread through waterbirds (Coughlan et al. 2017c). For invasive species, they may undergo secondary

dispersal through biotic and abiotic vectors like floodwaters, invertebrates and waterbirds, accelerating invasions in hydrologically connected systems (Lovas-Kiss et al. 2018; Navarro-Ramos et al. 2021). Furthermore, frequent short-distance movements, such as daily foraging flights, sustain propagule pressure and gene flow between subpopulations. Mallards visiting multiple wetlands within a single day may carry eggs at each site, creating a dispersal network that enhances invasion potential (Kleyheeg et al. 2017). While large egg size reduces survival during gut transit, it promotes local retention and repeated colonization of adjacent habitats through stepping-stone dispersal (Coughlan et al. 2017b).

Our experiment quantified endozoochory of apple snail eggs under controlled conditions, may not fully represent the natural diet, where waterbirds consume mixed plant-animal food. A higher proportion of eggs may potentially survive gut passage, and have longer retention time, when birds feed on a higher fibre diet dominated by plant material, instead of animal-based diet. Crustacean eggs showed higher survival in mallards when mixed with a plant-based than an animal-based diet, and markers had a longer gut retention time on the plant-based diet (Charalambidou et al. 2005). Furthermore, epizoochory, the transport of organisms externally attached to birds via their feathers, feet or bills, provides an additional potential dispersal pathway for apple snails. A review highlights this external dispersal mechanism by various waterbirds (Coughlan et al. 2017a). Molluscs such as bivalves, gastropods, and barnacles can attach to the external surfaces of waterbirds like gulls, shorebirds, and ducks for extended periods (Coughlan et al. 2017c; Green et al. 2023). Recent studies demonstrate that invertebrate eggs also adhere to waterbirds for passive transport as well. For example, cladoceran ephippia can attach to duck legs (Wang et al. 2023), and aquatic insects lay eggs on the leg of waterbirds (Carbonell et al. 2020).

In conclusion, our findings reveal that regurgitation and defecation by waterbirds can facilitate the spread of a highly invasive snail. While waterbirds can reduce the abundance of apple snails through predation, their regurgitation facilitates short-distance dispersal of viable eggs in pellets, and defecation enables long-distance dispersal of fewer eggs within faeces. Waterbird-mediated dispersal of alien species, which has often been an overlooked pathway of biological invasions, should be taken into account if management strategies are to be effective (Reynolds et al. 2015; Green 2016; Reynolds et al. 2017).

Author contribution

YZ: Methodology, Data Curation, Formal analysis, Writing – Original, Visualization; QZ: Methodology; AG: Writing - Review and Editing, Supervision; ST: Supervision, Project administration, Funding Acquisition; XJ: Conceptualization; Resources; Writing - Review and Editing; Supervision; Project administration, Funding Acquisition.

Acknowledgments

Some assistance was provided by the Yangtze Delta Estuarine Wetland Ecosystem Observation and Research Station, Ministry of Education and the Shanghai Science and Technology Committee, Shanghai, China.

Funding declaration

XD was supported by Shanghai Environmental Monitoring Center (HT2024306A2), National Nature Science Foundation of China (32470556,

32301413 and 32401398), Science and Technology Commission of Shanghai Municipality (21DZ1200900, 22DZ1202600, and 19ZR1416200). AJG was supported by the Ministerio de Ciencia e Innovación WaterZoo project (PID2020-112774GB-I00 / AEI / 10.13039/501100011033). YZ was supported by the China Scholarship Council (202206140024).

References

Bellard C, Cassey P, Blackburn TM (2016) Alien species as a driver of recent extinctions. Biology Letters 12: 20150623. https://doi.org/10.1098/rsbl.2015.0623

Bertolero A, López MA, Rivaes S, Vigo M, Navarro J (2022) Identifying potential predators of the apple snail in the most important invasion area of Europe. Hydrobiologia 849: 4377–4389. https://doi.org/10.1007/s10750-022-04996-5

Bertolero A, Navarro J (2018) A native bird as a predator for the invasive apple snail, a novel rice field invader in Europe. Aquatic Conservation: Marine and Freshwater Ecosystems 28: 1099–1104. https://doi.org/10.1002/aqc.2917

Brola TR, Dreon MS, Fernández PE, Portiansky EL, Heras H (2021) Ingestion of poisonous eggs of the invasive apple snail adversely affects bullfrog intestine morphophysiology. Malacologia 63: 171–182. https://doi.org/10.4002/040.063.0202

Carbonell JA, Céspedes V, Green AJ (2020) Is the spread of the alien water boatman *Trichocorixa verticalis verticalis* (Hemiptera, Corixidae) aided by zoochory and drought resistant eggs? Freshwater Biology 66: 409–420. https://doi.org/10.1111/fwb.13647

Céspedes V, Bernardo-Madrid R, Picazo F, Vilà M, Rubio C, García M, Sanz I, Gallardo B (2024) Massive decline of invasive apple snail populations after blue crab invasion in the Ebro River, Spain. Biological Invasions 26(8): 2389–2395. https://doi.org/10.1007/s10530-024-03334-1

Charalambidou I, SantamarÍA L, Jansen C, Nolet BA (2005) Digestive plasticity in Mallard ducks modulates dispersal probabilities of aquatic plants and crustaceans. Functional Ecology 19: 513–519. https://doi.org/10.1111/j.1365-2435.2005.00998.x

Coughlan NE, Kelly TC, Davenport J, Jansen MAK (2017a) Up, up and away: bird-mediated ectozoochorous dispersal between aquatic environments. Freshwater Biology 62: 631–648. https://doi.org/10.1111/fwb.12894

Coughlan NE, Kelly TC, Jansen MAK (2017b) "Step by step": high frequency short-distance epizoochorous dispersal of aquatic macrophytes. Biological Invasions 19: 625–634. https://doi.org/10.1007/s10530-016-1293-0

Coughlan NE, Stevens AL, Kelly TC, Dick JTA, Jansen MAK (2017c) Zoochorous dispersal of freshwater bivalves: an overlooked vector in biological invasions? Knowledge & Management of Aquatic Ecosystems 418: 42. https://doi.org/10.1051/kmae/2017037

Estebenet AL, Martin PR (2002) *Pomacea canaliculata* (Gastropoda: ampullariidae): Life-history traits and their plasticity. Biocell 26: 83–89.

García-Alvarez A, van Leeuwen CHA, Luque CJ, Hussner A, Vélez-Martín A, Pérez-Vázquez A, Green AJ, Castellanos EM (2015) Internal transport of alien and native plants by geese and ducks: an experimental study. Freshwater Biology 60: 1316–1329. https://doi.org/10.1111/fwb.12567

Global Invasive Species Database (2024) Species profile: *Pomacea canaliculata*. http://www.iucngisd.org/gisd/species.php?sc=135

Green AJ, Lovas-Kiss Á, Reynolds C, Sebastián-González E, Silva GG, van Leeuwen CHA, Wilkinson DM (2023) Dispersal of aquatic and terrestrial organisms by waterbirds: A review of current knowledge and future priorities. Freshwater Biology 68: 173–190. https://doi.org/10.1111/fwb.14038

Green AJ, Sanchez MI, Amat F, Figuerola J, Hontoria F, Ruiz O, Hortas F (2005) Dispersal of invasive and native brine shrimps *Artemia* (Anostraca) via waterbirds. Limnology and Oceanography 50: 737–742. https://doi.org/10.4319/lo.2005.50.2.0737

Green AJ, Sanchez MI (2006) Passive internal dispersal of insect larvae by migratory birds. Biology Letters 2: 55–57. https://doi.org/10.1098/rsbl.2005.0413

Green AJ (2016) The importance of waterbirds as an overlooked pathway of invasion for alien species. Diversity and Distributions 22: 239–247. https://doi.org/10.1111/ddi.12392

Hufbauer RA, Rutschmann A, Serrate B, Vermeil De Conchard H, Facon B (2013) Role of propagule pressure in colonization success: disentangling the relative importance of demographic, genetic and habitat effects. Journal of Evolutionary Biology 26: 1691–1699. https://doi.org/10.1111/jeb.12167

Horgan FG, Stuart AM, Kudavidanage EP (2014) Impact of invasive apple snails on the functioning and services of natural and managed wetlands. Science Oecologica 54: 90–100. https://doi.org/10.1016/j.actao.2012.10.002

Kleyheeg E, Treep J, de Jager M, Nolet BA, Soons MB (2017) Seed dispersal distributions resulting from landscape-dependent daily movement behaviour of a key vector species, *Anas platyrhynchos*. Journal of Ecology 105: 1279–1289. https://doi.org/10.1111/1365-2745.12738

Kleyheeg E, van Leeuwen CHA (2015) Regurgitation by waterfowl: An overlooked mechanism for long-distance dispersal of wetland plant seeds. Aquatic Botany 127: 1–5. https://doi.org/10.1016/j.aquabot.2015.06.009

Laux JJ, Kölsch G (2014) Potential for passive internal dispersal: Eggs of an aquatic leaf beetle survive passage through the digestive system of mallards. Ecological Entomology 39: 391–394. https://doi.org/10.1111/een.12097

Liang K, Zhang J, Fang L, Zhao B, Luo M, Parajuli P, Ouyang Y (2013) The biological control of *Pomacea canaliculata* population by rice-duck mutualism in paddy fields. Biocontrol Science and Technology 23: 674–690. https://doi.org/10.1080/09583157.2013.790933

Liu C, Zhang Y, Ren Y, Wang H, Li S, Jiang F, Yin L, Qiao X, Zhang G, Qian W, Liu B, Fan W (2018) The genome of the golden apple snail *Pomacea canaliculata* provides insight into stress tolerance and invasive adaptation. Gigascience 7: 1–13. https://doi.org/10.1093/gigascience/giy101

Lovas-Kiss Á, Navarro-Ramos MJ, Vincze O, Löki V, Urgyán R, Pallér-Kapusi F, van Leeuwen CHA, Green AJ, Lukács BA (2023) Traits for transport: Alien wetland plants gain an advantage during endozoochorous seed dispersal by waterfowl. Freshwater Biology 68: 1703–1715. https://doi.org/10.1111/fwb.14154

Lovas-Kiss Á, Sanchez MI, Molnar AV, Valls L, Armengol X, Mesquita-Joanes F, Green AJ (2018) Crayfish invasion facilitates dispersal of plants and invertebrates by gulls. Freshwater Biology 63: 392–404. https://doi.org/10.1111/fwb.13080

Lovas-Kiss Á, Vincze O, Löki V, Pallér-Kapusi F, Halasi-Kovacs B, Kovacs G, Green AJ, Lukacs BA (2020) Experimental evidence of dispersal of invasive cyprinid inside migratory waterfowl. Proceedings of the National Academy of Sciences of the United States of America 117: 15397–15399. https://doi.org/10.1073/pnas.2004805117

Machado-Stredel F, Atauchi PJ, Nuñez-Penichet C, Cobos ME, Osorio-Olvera L, Khalighifar A, Peterson AT, Fletcher RJ (2024) The roles of abiotic and biotic factors in driving range shifts: An invasive *Pomacea* snail facilitates *Rostrhamus sociabilis* (Snail Kite) northward range expansion. Ornithology 141(3): ukae022. https://doi.org/10.1093/ornithology/ukae022

Martín-Vélez V, Sanchez MI, Lovas-Kiss Á, Hortas F, Green AJ (2021) Dispersal of aquatic invertebrates by lesser black-backed gulls and white storks within and between inland habitats. Aquatic Sciences 84: 10. https://doi.org/10.1007/s00027-021-00842-3

Navarro-Ramos MJ, Green AJ, Lovas-Kiss A, Roman J, Brides K, van Leeuwen CHA (2021) A predatory waterbird as a vector of plant seeds and aquatic invertebrates. Freshwater Biology 67: 657–671. https://doi.org/10.1111/fwb.13870

Reynolds C, Cumming GS, Vilà M, Green AJ (2017) Birds as key vectors for the dispersal of some alien species: Further thoughts. Diversity and Distributions 23: 577–580. https://doi.org/10.1111/ddi.12549

Reynolds C, Miranda NAF, Cumming GS (2015) The role of waterbirds in the dispersal of aquatic alien and invasive species. Diversity and Distributions 21: 744–754. https://doi.org/10.1111/ddi.12334

Tesson SVM, Weissbach A, Kremp A, Lindstrom A, Rengefors K (2018) The potential for dispersal of microalgal resting cysts by migratory birds. Journal of Phycology 54: 518–528. https://doi.org/10.1111/jpy.12756

Urgyán R, Lukács BA, Fekete R, Molnár VA, Nagy A, Orsolya V, Green AJ, Lovas-Kiss Á (2022) Plants dispersed by a non-frugivorous migrant change throughout the annual cycle. Global Ecology and Biogeography 32: 70–82. https://doi.org/10.1111/geb.13608

Wang Z, Xu S, Luo C (2023) Attachment and release of water fleas' ephippia on a medium-sized waterfowl's leg for migration. Langmuir 39: 12402–12411. https://doi.org/10.1021/acs.langmuir.3c01563

Wu ZY, Milne RI, Liu J, Nathan R, Corlett RT, Li DZ (2023) The establishment of plants following long-distance dispersal. Trends in Ecology and Evolution 38: 289–300. https://doi.org/10.1016/j.tree.2022.11.003

Supplementary material 1

Retention & hatching rate of apple snail eggs in 19 male mallard feeding trials

Author: Xiaodong Jiang

Data type: xlsx

Explanation note: This dataset encompasses retention time measurements of intact apple snail eggs retrieved from the faeces and regurgitated pellets of eight male mallards across 19 feeding trials. Additionally, it includes hatching rate comparisons between control apple snail eggs and those recovered from the same biological samples in the identical trials.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3391/ai.2025.20.4.175069.suppl1