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Bird-mediated endozoochory as a potential dispersal mechanism of bony fishes

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Ecography
2024: e07124
doi: 10.1111/ecog.07124
Subject Editor: Thierry Oberdorff
Editor-in-Chief: Miguel Araújo
Accepted 2 February 2024

Keywords: bony fish, endozoochory, fish dispersal

The dispersal of fish into distant and isolated habitats remains a topic of continuous discussion in the field of fish biogeography. This is particularly relevant due to the perceived limitation of fish movement to what is known as active dispersal. Fish migration is often confined to interconnected water bodies, underscoring the significance of dispersal for fish inhabiting isolated aquatic habitats. However, empirical evidence for a natural (i.e. not human-mediated) mechanism has been limited. Here we explore and provide evidence for waterbird-mediated endozoochory as a possible dispersal mechanism in various fish species and families. We force-fed mallards *Anas plathyrynchos* with fertilised eggs of nine bony fish species, covering nine taxonomic families. We recovered viable embryos of five fish taxa in the faeces of mallard, proving the ability of fish eggs to survive the passing of the digestive system of waterbirds. Moreover, the recovered eggs successfully hatched into larvae in two fish species. Taking into the flight speed and numerosity of mallards, as well as the high abundance of fish eggs, our results highlight endozoochory of fish eggs by waterbirds as a possible significant, although likely rare natural dispersal mechanism that can occur across more species than previously known in freshwater fish.

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Fish dispersal plays a significant role in shaping aquatic ecosystems and community structures, but also in influencing fundamental processes such as nutrient cycling, food webs, and habitat structures. For instance, dispersal of native fish is a crucial mechanism sustaining the complexity and resilience of local fish communities. In contrast, the dispersion of different fish taxa can pose significant threats to aquatic communities (e.g. homogenization: Rahel, 2000, Rahel, 2002). Understanding dispersal processes, particularly movement between isolated water networks, is essential for comprehending aquatic ecosystem dynamics and guiding effective conservation and restoration efforts. One critical aspect in understanding the dispersal potential of fishes is deciphering whether waterbirds may serve as dispersal vectors for fish (Green et al. 2023). This is particularly important, since waterbirds preferentially consume fish eggs (Street 1977, Bayer 1980) and can easily move across water networks. Recent genetic studies suggest that these events are possible, as suggested in the case of perch *Perca fluviatilis* (Garcia et al. 2023). Furthermore, empirical evidence has emerged from two distinct experimental investigations demonstrating the survivability of fish eggs passing through the digestive tracts of waterbirds (Silva et al. 2019, Lovas-Kiss et al. 2020).

Silva et al. (2019) showcased the resistance of highly durable eggs of killifish (*Austrolebias* sp.), surviving intact for up to 30 h of avian digestion. Similarly, Lovas-Kiss et al. (2020) showed that even species of cyprinids harbouring delicate eggs (*Cyprinus carpio*, *Carassius gibelio*) were able to hatch after traversing a waterbird's digestive system, highlighting endozoochory as a possible dispersal mechanism in these taxa. While these studies have spotlighted the potential mechanism of endozoochory as a facilitator of fish dispersion, their scope remained confined to cyprinid fishes. Therefore, in this study, our objective was to extend on this investigation and explore the possibility of endozoochorous dispersal of nine freshwater fish species from nine taxonomic families.

Fertilized eggs from a total of nine fish species, approximately at the morula stage, were administered to captive mallards through force-feeding. Subsequently, faecal samples were collected at specific time intervals and were subjected to visual scrutiny to detect the presence of fish eggs. Passing rate of eggs varied substantially among fish taxa. Among the nine species subjected to testing, we recovered intact eggs with live embryos in six taxa (Table 1).

Remarkably, only three species: the grass carp *Ctenopharyngodon idella*, amur sleeper *Perccottus glenii* and pike-perch *Sander lucioperca* had no egg passage. Among the examined taxa, the pumpkinseed *Lepomis gibbosus* exhibited the highest egg passage rate, with 29 intact eggs identified, equivalent to 0.18% of the total number of force-fed eggs. With four eggs (0.1%), the second highest passage rate was observed in the case of the stone moroko *Pseudorasbora parva*. We observed a similar passage rate (0.03%) comparing tench *Tinca tinca* with five eggs and Wels catfish *Silurus glanis* with two eggs. With one and three passed eggs (0.01 and 0.009%, respectively) the common carp and the hybrid African catfish *Clarias gariepinus* × *Heterobranchus longifilis* displayed the lowest passage rate.

Table 1. Fish species and families used for the experiment, with the egg fertility rate of the fed eggs, number of eggs used for the experiment. Number of duck individuals with intact egg passage. Passage time of the survived eggs, living embryos in brackets. Total number of hatched eggs.

Fish species	Family	Egg fertility (%)	Number of fed eggs per duck	Number of ducks used	Number of ducks passing viable eggs	1 h	2 h	4 h	8 h	12 h	Total passed eggs	Living embryo in them	Hatched
Hybrid African catfish – *Clarias gariepinus* × *Heterobranchus longifilis*	Clariidae	100	4000	8	1		3(1)				3	1	0
Grass carp – *Ctenopharyngodon idella*	Xenocyprididae	100	4000	8	–						0	–	–
Common carp – *Cyprinus carpio*	Cyprinidae	100	1000	8	1	1(1)					1	1	0
Pumpkinseed – *Lepomis gibbosus*	Centrarchidae	53	2000	8	3	24(5)	3(2)	1(0)	1(0)		29	7	0
Amur sleeper – *Perccottus glenii*	Odontobutidae	100	1700	1	–						0	–	–
Stone moroko – *Pseudorasbora parva*	Gobionidae	100	1000	4	1	4(2)					4	2	1
Pike-perch – *Sander lucioperca*	Percidae	100	500	8	–						0	–	–
Wels catfish – *Silurus glanis*	Siluridae	100	750	8	1	2(0)					2	0	0
Tench – *Tinca tinca*	Tincidae	100	2000	8	3	4(4)	1(1)				5	5	3

We observed the highest hatching in two species, from which the tench had the highest hatching rate with 60% (three eggs, all of them contained living embryos). The second species where hatching of passed eggs was observed was the stone moroko, but only one of their passed eggs hatched (25%, two of the eggs carried viable embryos). Despite the high passage rate in the case of pumpkinseed, only seven contained living embryos and none of them hatched due to a fungal infection. None of the passed eggs of common carp, hybrid African catfish, and the Wels catfish hatched, but we observed living embryos in the passed eggs of the first two.

Notably, in the experiments involving multiple ducks, it was observed that passage rate is highly heterogeneous among ducks, most often with only a single mallard individual (but not the same individual among experiments) passing eggs. Additionally, there were two cases when three ducks had passed eggs. In three fish species, egg passage was observed within two hours after force-feeding for three species, while the pumpkinseed exhibited egg passage even between four and eight hours after feeding. Importantly, all birds were monitored closely after force-feeding, no regurgitation was noted and all recovered eggs were clearly embedded in faecal material.

In summary, our study found that 66% (six out of nine) of the tested fish species were capable of passing through the digestive tract of mallards, from which two (stone moroko and tench) hatched. These results suggest that dispersal facilitated by waterbirds, through endozoochory, may represent a significant and possibly widespread mechanism for the dispersal of bony fishes. However, it is crucial to note that the egestion of eggs occurred at low rates in each trial, indicating that the transport of viable fish embryos through endozoochory might be infrequent. Comparing the passage rates of the carp to a previous paper (Lovas-Kiss et al. 2020), we recovered significantly fewer passed eggs in the current experiment. This could be explained by several factors, such as the individual variability in the digestion process in mallards. Alternatively, the quality of the eggs might have differed between the two experiments. The success of such transport in natural settings could be further hindered by factors such as the probability of reaching suitable habitats, or factors influencing hatchability, such as fungal infections. Nevertheless, during spawning events, the quantity of fish eggs can be substantial, mirroring the density and diversity of waterbirds (Wetlands International 2023) that exhibit a clear preference for consuming them. Given these large numbers, even relatively rare instances of successful transport of viable fish embryos can significantly contribute to gene flow, especially when occurring between isolated water networks, even if the distances involved are minimal (Lovas-Kiss et al. 2021).

Mallards engage in significant daily movements even outside the migration period, often covering distances exceeding 10 km (Bengtsson et al. 2014, Kleyheeg et al. 2017). Mallards have been observed to move between isolated wetlands at speeds of approximately 80 km/h even during the breeding period (Urgyán et al. 2023). Most egested fish eggs in our experiment were passed within one hour post-feeding, corroborating previous research (Lovas-Kiss et al. 2020) and suggesting a potential dispersal distance of up to 70 to 90 km in these fish. While the hatching rates of passed eggs were highly compromised by fungal infections in our experiment, the passage of eggs of multiple fish species with living embryos highlights the significant potential for endozoochorous dispersal by waterbirds as a crucial mechanism for fish to reach and colonise new habitats. Further investigation with a larger sample size of passed eggs is needed to clarify associations between egg traits and survival.

Acknowledgements – We are grateful to the following people for their work in the field and in the laboratory: Tamás Abonyi, Dénes Bajcsev-Dancsó, László Nagy, Tibor Orcsik, Zoltán Sallai, Ifeanyi Emmanuel Uzochukwu, Csaba Weber, Uroš Ljubobratović, Gyula Kovács, and Jenő Káldy.

Funding – The experiment was financed by NKFIH OTKA FK-138698 and FK-127939 grants. BAL, ÁL-K, LA and OV were supported by the János Bolyai Research Scholarship of the Hungarian Academy of Sciences. Researchers were supported by the ÚNKP-23-3-II (DS) and ÚNKP-23-5 (BAL, ÁL-K, LA) New National Excellence Program of the Ministry for Culture and Innovation from the National Research, Development and Innovation Fund. Project no. TKP2021-NKTA-32 was implemented with the support provided from the National Research, Development and Innovation Fund of Hungary, financed under the TKP2021-NKTA funding scheme. DS was supported by the PhD Excellence Scholarship from the Count Tisza Foundation for the University of Debrecen. The work of OV was supported by the National Scientific Research Fund (OTKA K143421). The research presented in the article was carried out within the framework of the Széchenyi Plan Plus program with the support of the RRF 2.3.1-21-2022-00008 and GINOP_PLUSZ-2.1.1-21-2022-00245 projects. This project has been implemented with the support of the Ministry of Culture and Innovation of Hungary from the National Research, Development and Innovation Fund, financed under the Cooperative Doctoral Program (RH/527-20/2021) funding scheme. This work was supported by the European Union-NextGenerationEU, through the National Recovery and Resilience Plan of the Republic of Bulgaria, project No BG-RRP-2.004-0001-C01, DUECOS.

Permits – The experiment was approved by the scientific and ethical committee of the Babeş-Bolyai University, Cluj Napoca.

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Transparent peer review

The peer review history for this article is available at https://publons.com/publon/10.1111/ecog.07124.

Data availability statement

All data used in the paper are available in Table 1 and the Supporting information.

Supporting information

The Supporting information associated with this article is available with the online version.

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