

Evolutionary transitions in parental care in vertebrates

PD_132819, Final report – Dr Balázs Vági, 31 January 2024

Executive summary

This NKFIH project aimed at understanding the evolution and diversification of parental care, one of the most striking behaviours in vertebrates, the dominant clade of the Earth's biosphere. Me and my cooperators made significant progress in this field, which we published in top scientific journals and presented at various conferences, and also to the wider public via press release and other popularization. In terms of career development, the principal investigator (PI) became a well-recognized member of the international community of evolutionary biologists and herpetologists, and the execution of the project also helped the education of many undergraduate students and remained a key component of international cooperations between the University of Debrecen and other prestigious universities worldwide. We also built unparalleled, detailed databases on parental care and brain size which can be the basement for future research. Below, I briefly present our main achievements. The presentation of the scientific results follows the structure of the original research proposal.

Summary of project achievements

I. Directions of transitions between parental care forms in vertebrates

1. Our first hypotheses investigated if the pattern of transitions among parental care types in vertebrates follow the so-called **stepping-stone hypothesis**, which states that male parental care evolved first from male territoriality, followed by the evolution of biparental care, which could then simplified to female care. We did not find support for this overall pattern. According to our results, the evolution of male and female uniparental care was similarly likely both in ray-finned fishes and in amphibians, although the desertion of males often indeed gave rise to female-only care from biparental care (Vági *et al.* 2020; 2022, Vági *et al.* submitted, Vági *et al.* MSb).
2. The second hypothesis investigated if there is a **reinforcement** between the evolution of care in the two sexes, i.e. if the evolution of (more) male care gives rise to the evolution of (more) female care. Here we find an opposing pattern between early (anamniotic) and derived (amniotic) vertebrates. The latter, birds and mammals indeed show a positive correlation between male and female care, however, fish and amphibians where care is predominantly uniparental, show a negative correlation (Vági *et al.* MSb).
3. The third hypothesis investigated if there is more **nourishment** of the offspring in females than in males. We could confirm this pattern in amphibians, reptiles, bony and cartilaginous fish and in mammals (Vági *et al.* 2020; 2022; Katona *et al.* 2023; Vági *et al.* submitted, Vági *et al.* MSb).
4. Lastly, we asked if **complex care forms** can easily lost and evolve back to simple forms. We had to refine this proposed pattern according to our new results. We find that simple care forms are evolutionary labile. While, in contrast, when complex anatomical and physiological adaptations also evolve along specialised care forms, these can stabilise parental care (Katona *et al.* 2023; Vági *et al.* submitted).

II. Predictors of parental care

1. We confirmed **fertilization mode** as a key component of parental care evolution in both vertebrate groups which show remarkable variation in this term: tailed amphibians (Caudata – *Vági et al. 2022*) and ray-finned fish (Actinopterygii – *Vági et al. submitted*). In both groups, the sex which takes control over the fertilization process will be the sole or the dominant care provider.
2. We identified **breeding system and sexual selection** as key predictors of care evolution. Despite that amphibians are very sensitive to abiotic environmental conditions in all stages of their development, it seems that breeding systems and sexual selection played a more important role in their care evolution than the abiotic environment (*Vági et al. 2020*). While in reptiles, care is mostly uniparental by the female, we identified surprising new associations between components of their breeding system, i.e. sexual size dimorphism and sex determination (*Katona et al. 2021*) and multiple paternity, adult sex ratios and sex determination (*Pipoly et al. 2023*).
3. Regarding **life history**, we found that parental care is associated with fewer offspring in salamanders (*Vági et al. MSa*) and in sharks and rays (*Katona et al. 2023*). We also detected evolutionary rigid total reproductive output in salamanders regardless parental care expenditure (*Vági et al. MSa*).
4. To test the influence of **cognitive abilities** on parental care, we built the largest dataset on brain size to date (*Mándi et al. MS*). Preliminary analyses show idiosyncratic patterns between care complexity and brain size (*Mándi et al. thesis*).

III. How the extent and complexity of parental care influence macroevolutionary patterns and species persistence?

1. Investigating **macroevolutionary patterns**, we identified a tendency of increasing care complexity in the phylogeny of vertebrates. This means that care forms in various life stages of the offspring are positively associated in both sexes (*Vági et al. submitted*) and that shorter care forms tend to give rise to longer care (*Vági et al MSb*). However, this pattern is not general to all vertebrate lineages: in ray-finned fishes, longer parental care tended to simplify into shorter forms both in males and in females (*Vági et al submitted*).
2. We found that, contrary to our expectations, IUCN **conservational threat status** is positively associated with parental care complexity in frogs, meaning that species with more complex care forms are more threatened with extinction (*Vági: abstract to WCH10*). Interestingly, this result is not applicable for tailed amphibians which have relatively simple care: here, threat status and the presence of egg attendance are not associated (*Angelusz & Vági: abstract to WCH10*).

Career development

Me as **PI, Dr Balázs Vági** made substantial career development executing the project. My publication record strengthened with 4 papers and an invited book chapter as first or last author. My citation number almost doubled. I built several international cooperations which opened new, now ongoing research projects. I was invited to give multiple lectures in seminars or conferences, became a regular reviewer of peer-reviewed international journals and NKFIH reports, and juried students' (TDK) presentations as an invited jury member. I became a supervisor at Juhász-Nagy Pál Doctoral School of the University of Debrecen (UD). These achievement contributed to my consideration as a core team member of the newly established Biodiversity, Climate Change and Water Management Coordination Research Centre at UD and participation in the educational

board of the starting new English PhD programme on Conservation. I successfully applied for a conference grant at the Hungarian Academy of Sciences and also completed a Lendület Starting proposal which will, in case of successful application, create funding for follow-up research.

The project also helped the progress of several **students** at UD and elsewhere. *Gergely Katona* (UD) completed all publications necessary for defending his PhD thesis. *Mihály Mándi* (UD) successfully defended his BSc thesis, supervised by the PI, and started an MSc in Biology, also with PI's supervision. He also participated in two Hungarian Ethologists' Meeting and won a 2nd place at UD's students' (TDK) conference. *Petra Somogyvári* (UD), supervised by the PI, defended her MSc thesis and successfully applied to continue this work as a PhD in UD, but decided not to start it for personal consideration. *Boldizsár Paládi-Kovács* (University of Oxford from Oct 2023) started a research project with the supervision of the PI. *Ábel Angelusz* (ELTE Radnóti Miklós School) will attend a research students' conference (TUDOK) and applied for a conference grant with a research associated with the current project and supervised by the PI. Three students from the University of Bath (*Daniel Marsh*, *Julian Hochstein-Mintzel*, *Josephine Darling*) completed successful short-term placement projects which contributed to our parental care research.

Cooperations

The project established successful cooperations with both senior and early-career researchers in other institutes in Hungary and in abroad. I cooperated with *Prof András Liker* and his group at Univ. of Pannonia (*Dr Ivett Pipoly*); *Prof Zsolt Végvári* (HUN-REN Institute of Aquatic Ecology); *Dr Veronika Bókonyi* (HUN-REN Plant Protection Institute). I continued collaboration with *Prof Robert P Freckleton* (Univ of Sheffield, UK) and *Prof Tamás Székely* (Univ of Bath, UK). Results from this project contributed to the recognition of Prof Freckleton as an honorary professor at Biodiversity, Climate Change and Water Management Coordination Research Centre, UD. Cooperation with *Prof Matthew Wills* and *Andrew Brinkworth* (University of Bath, UK) continued and culminated in a proposal for a Leverhulme Research Project Grant with the leading of Prof Wills, and the PI as a collaborator. We also continued cooperation of the groups of *Profs JF Lemaître and JM Gaillard* (CNRS Lyon). Our research induced a new and now ongoing project with *Prof Hans Hofmann* (Univ of Texas at Austin) and *Dr Mark Wilkinson* (Natural History Museum London). These collaborations were supported by visit of the PI in the UK (28 Nov – 21 Dec 2022) and visits of Profs Freckleton and Hofmann in Debrecen.

Outreach and popularization

The PI held four **invited lectures** associated with the project:

Vági B: Amphibians in the focus: evolutionary biology and conservation. Research seminar of the Danube Research Institute, Centre for Ecological Research, MTA (Febr 2020)

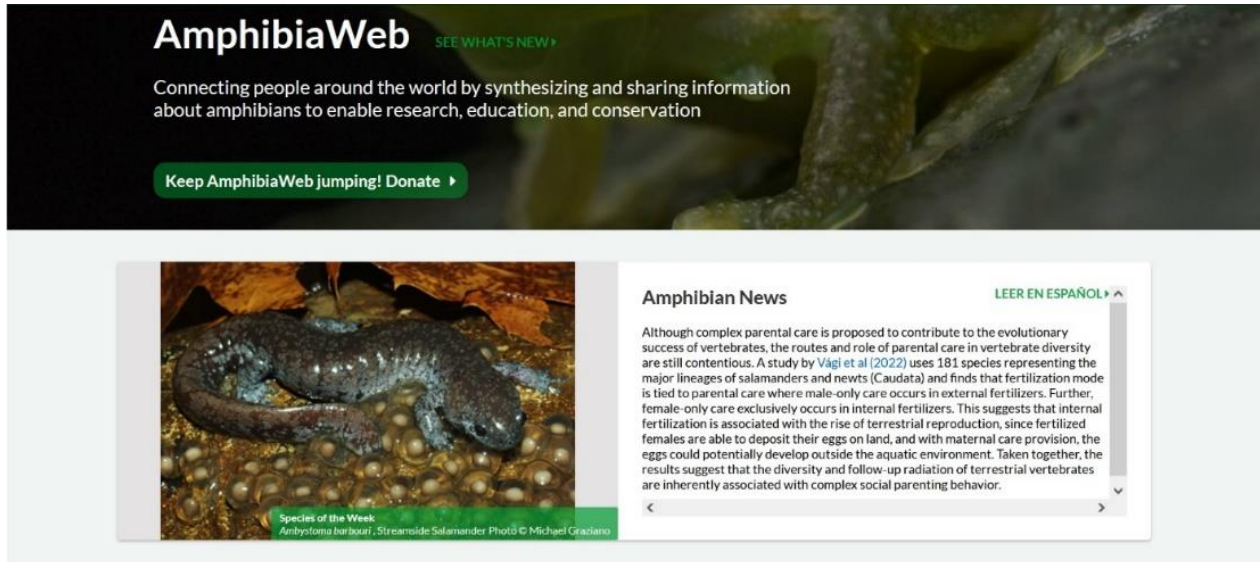
Székely T & Vági B*: Reproductive strategies in the animal kingdom: from evolutionary biology to conservation Day of Science, Nov 2022, UD *held by PI

Vági B, Freckleton RP, Székely T: Reproductive strategies and parental care in basal vertebrates – invited talk (online) at Beijing Normal University, China, 16 Dec 2022

Balázs Vági: From mate choice in frogs to the evolution of reproductive strategies. Kolozsvár/Cluj Biologists' Days, plenary talk (in Hungarian). April 2023

We also popularized our research via several **press release** (e.g. websites of UD and Hun-REN ÖK; 24.hu; Turista Magazin; Klubrádió) and in the yearly **Researchers' Night** at UD. One of our publications was highlighted in Amphibiaweb, the largest worldwide scientific information website on amphibians (Figure 1). Tim Vernimmen, an independent journalist from the Netherlands, is also working on a report popularizing our research, in context to other related international amphibian research.

Figure 1. Vági et al. 2022 as a highlighted publication in Amphibiaweb



Publications emerged from the project

Published research papers

Katona G, Szabó F, Végvári Z, Liker A, Freckleton RP, Vági B*, Székely T. Evolution of reproductive modes in sharks and rays. *Journal of Evolutionary Biology* 36:1631-1640 (2023)

*PI is a joint senior author

Pipoly I, Duffy R, Mészáros G, Bókony V, Vági B, Székely T, Liker A: Multiple paternity is related to adult sex ratio and sex determination system in reptiles. *Journal of Evolutionary Biology* 36:935-944 (2023)

Vági B, Marsh D, Katona G, Végvári Z, Freckleton RP, Liker A, Székely T. The evolution of parental care in salamanders. *Scientific Reports* 12:1-9 (2022)

Katona G*, Vági B*, Végvári Z, Liker A, Freckleton RP, Bókony V., Székely T: Are evolutionary transitions in sexual dimorphism related to sex determination in reptiles? *Journal of Evolutionary Biology* 34:594-603. (2021)

*PI is a joint first author

Vági, B.*, Végvári, Z.*, Liker, A., Freckleton, R.P., Székely, T. Climate and mating systems as drivers of global diversity of parental care in frogs. *Global Ecology and Biogeography* 29:1373-1386 (2020)

*PI is a joint first author

Submitted manuscripts

Vági B, Katona G, Miranda OG, Mándi M, Plagányi E, Végvári Z, Liker A, Hofmann H, Freckleton RP, Székely T: The evolution of the diversity in parental care and fertilization modes in ray-finned fishes. Submitted to *Evolution* Jan 2024

Garcia-Miranda O, Colchero F, Valdebenito JO, Cortez D, Conde DA, Pipoly I, Liker A, Vági B, Bertelsen MF, Kilili A, Urrutia AO, Székely T: Evolutionary insights into birth sex ratios: Evidence from 90 species of birds and 315 species of mammals. Submitted to *Journal of Evolutionary Biology* Oct 2023

Manuscript under revision by the authors and before resubmission

Vági B, Marsh D, Végvári Z, Wilkinson M: The evolution of reproductive strategies in salamanders. Submitted, but rejected in *Global Ecology and Biogeography*. To be submitted to *American Naturalist* in Febr 2024 (Vági et al. MSa)

Manuscripts in preparation

Vági B, Freckleton RP, Liker A, Székely T: The evolution of the diversity of parental care in vertebrates (Vági et al. MSb)

Mándi M, Hofmann H, Vági B: VerteBrainData: A comprehensive brain size database for 6500 vertebrate species. To be submitted to *Scientific Data* (Mándi et al. MS)

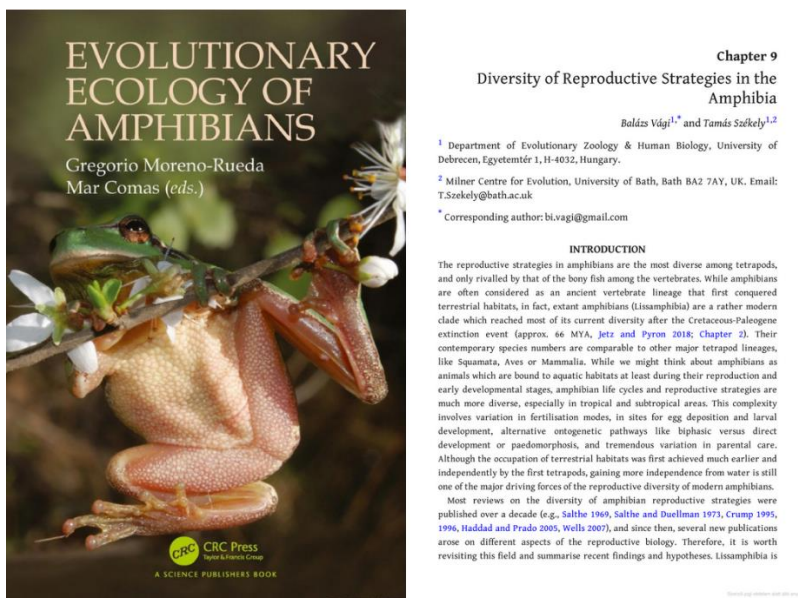
Figure 2. Research paper front covers associated with (from left to right): Vági et al. 2020; Katona et al. 2021; Pipoly et al. 2023; Katona et al. 2023.



Book chapter

Vági B & Székely T: Diversity of reproductive strategies in the Amphibia. In *The Evolutionary Ecology of Amphibians*, editors G Moreno-Rueda & M Comas, CRC Press (2023) (Figure 3)

Figure 3. The front cover of Moreno-Rueda & Comas (2023), and the chapter by Vági & Székely



Contribution to conferences, workshops, symposia

2020

Vági B, Végvári Z, Marsh D, Katona G, Liker A, Freckleton RP, Székely T: Evolution of terrestrial reproduction in salamanders. Hungarian Ethologists' Meeting MET, online (talk)

2021

Vági B, Marsh D, Végvári Z, Wilkinson M: How egg-laying sites and juvenile habitats influence reproductive output and its trade-offs in salamanders? Hungarian Ethologists' Meeting MET, online (talk)

2022

Vági B, Freckleton RP, Székely T: Reproductive strategies and parental care in basal vertebrates The evolution of complexity meeting, University of Bath 28-29 July, Bath (talk)

Vági B, Marsh D, Végvári Z, Wilkinson M: How reproductive strategies affect reproductive output in salamanders – poster presentation at the conference of European Society of Evolutionary Biology ESEB 14-19 August, Prague (poster)

Mihály Mándi & Balázs Vági „Brain size and parental care in vertebrates” Hungarian Ethologists' Meeting MET, Budapest 25-27 Nov 2022 (talk)

2023

Mándi M: A comprehensive brain size database for 6500 vertebrate species and its applications” Autumn Students' Scientific Conference (TDK) at UD (talk, won 2nd place in competition)

Mándi M, Hofmann H, Vági B: VerteBrainData: A comprehensive brain size database for 6500 vertebrate species. Hungarian Ethologists' Meeting MET, Debrecen 26-28 Oct 2023 (poster)

To be presented in 2024

Vági B: The evolution of the diversity in parental care and fertilization modes in ray-finned fishes. To be presented in Sexual Selection Workshop 17-21 May, Erice, Italy.

Vági B: Frogs providing more complex parental care are at a greater risk of extinction. To be presented in 10th World Congress of Herpetology, Kuching, Malaysia

Vági B and Angelusz Á: The association between threat status, ecology and reproductive strategies in salamanders. To be presented in 10th World Congress of Herpetology, Kuching, Malaysia

Theses associated with the project:

Mándi M: The association between brain size and parental care in vertebrates (University of Debrecen, BSc in Biology, defended in 2023) *in Hungarian*

Somogyvári P: The association between adult sex ratios, mortality and maturation in reptiles (University of Debrecen, MSc in Biology, defended in 2023) *in Hungarian*

Research grant applications emerged from the project

The PI successfully applied for an *MTA conference grant* for his attendance in World Congress of Herpetology 2024. PI also submitted a proposal for a *Lendület* starting grant for follow-up studies induced by the current project in 2023, which did not gain support. A revised version of this proposal will be resubmitted in 2024. PI also participating in a *Leverhulme Research Project Grant* proposal (PI: Prof Matthew Wills) as collaborator, and in Prof Tamás Székely's successful *ELKH* (now *HUN-REN*)-UD group-starter proposal as a core team member.