

# Breeding system variation in vertebrates: the significance of adult sex ratios

K – 116310, Final report – Prof Tamás Székely, 28 January 2021

## Executive summary

The overarching objectives of this NKFIH project were to understand the causes and implications of adult sex ratio (ASR) variation in vertebrates. We made significant progress toward achieving these objectives. In addition, the NKFIH project gave us leverage to bring ASR into mainstream behavioural ecology research, and induce further research in evolutionary demography, population biology and organismal biology. Importantly, the NKFIH project produced a large database on vertebrate ecology, life history and behaviour (including sex ratio-related demographic variables), and this database will be an excellent springboard for future phylogenetic analyses. Also, the project facilitated the academic career of young Hungarian evolutionary biologists (Dr Ivett Pipoly and Dr Balázs Vági), and contributed to research and higher education at University of Debrecen and University of Pannonia.

## Summary of project achievements

### 1. Causes of ASR variation (H1-H3, see original Research Proposal)

Our project successfully identified sex specific differences in maturation age, juvenile and adult survival rates as the drivers of adult sex ratio (ASR) variation in multiple vertebrate groups (reptiles, birds, mammals). Our work has also uncovered novel associations between dispersal patterns and ASR in birds.

### 2. Implications for breeding systems (H4-H6)

Our team has carried out the most extensive analyses as yet in several vertebrate groups that produced three main results. First, in both birds and mammals we showed that intense sexual selection among males is related to female-biased ASR whereas female sexual selection is associated with male-biased ASR. This association is the opposite that was predicted by several evolutionary biologist including Charles Darwin. Second, by investigating ASR variation in reptiles, we confirmed previous analyses that ASR variation was different between reptiles with XY and ZW sex determination systems. Interestingly, genetic mating systems appears to be different between XY and ZW reptiles, suggesting a potential link to ASR variation. Third, in amphibians ASR variation was not associated with parental roles by males and females.

### 3. Macroevolutionary implications (H7-H9)

Our team has contributed to 2 major efforts to investigate macroevolutionary implications of sex ratio variation. First, we are members of the B10k consortium <https://b10k.genomics.cn/> that has produced full-genome sequences of over 300 bird species. The first results of B10k project was published in autumn 2020 in Nature, and follow up analyses are currently underway that targets uncovering the potential associations between bird genomes, demography and life histories. Second, we are collaborating with Species360 team to quantify ASR variation using 1000s of vertebrate species <https://www.species360.org/> Provisional results suggest that the ASR variation uncovered by Pipoly et al. (2015) is consistent with demographic data from captive species.

### 4. Additional results

The NKFIH-funded research that was published in Proc Roy Soc B (Vagi et al. 2019) lead to an NKFIH post-doctoral application by Dr Balázs Vági. The application was successful (PD 132819) so that Balázs

has 3 years to develop his own research program focused on parental care evolution in vertebrates. In addition, the ongoing contribution of Dr Ivett Pipoly in ASR variation in birds and mammals paved a way to her Marie Curie post-doctoral fellowship application. The results will be known in February 2021.

## **Research achievements in detail**

### **Birds**

- We compiled the most comprehensive ASR-related dataset in the world. The dataset includes nearly all extant bird species (ca 10,000 spp) and approximately 150 ecological, demographic and life history variables. ASR data are available for over 300 species.
- We investigated the relationship between mortalities, dispersal and ASR in birds (see H1, H2 & H3) and showed that natal dispersal and breeding dispersal follow different evolutionary patterns, and they are not related to mating system variation. However, ASR is a significant predictor of sex bias in dispersal behaviour (Végvári et al. 2018 Ecology & Evolution).
- We found a robust relationship between ASR and sex difference in maturation in birds (see H2). By using phylogenetic path analyses, the best fitting model showed that differences in mortalities and ASR drive sex-different maturation times, rather than vice versa (Ancona et al. 2020 Evolution Letters).
- By investigating the causes of ASR variation (H1-H3) in 6 plover populations we showed that ASR varies between these populations, and much of the variation is due to different juvenile survival (Eberhart-Phillips et al. 2018 Nature Communications).
- We demonstrated that mate fidelity (a potential predictor of ASR) may increase reproductive success in snowy plovers (Halimubieke et al. 2019 Ecology and Evolution).
- We analysed offspring sex ratios in Kentish plover, and showed that secondary sex ratios are not different from unity (Que et al. 2019 Journal of Ornithology).
- In a review paper we summarised and evaluated the significance of shorebirds in studies of ASR and breeding system (Székely 2019 Journal of Ornithology). This review explains the rationale that underpinned much of ASR research.
- We published a commentary on an ASR experiment (Kingma & Székely 2019 Current Biology).

### **Mammals**

- In collaboration with Prof JM Gaillard's group (CNRS, France), we analysed the sex difference in life history trajectories in mammals (H1-H3, Lemaitre et al. 2020 PNAS)
- In collaboration with Prof Gaillard, we have collated a detailed population-level database on ASR in mammals (Frederico et al., in prep) and currently checking the reliability of ASR estimates. Based on these data, we are planning a follow-up paper testing whether ASR predicts social organisation, mating systems and parenting in mammals (H4-H6).
- We showed that male parental care and social monogamy are correlated with a more male-biased ASR and a shorter lifespan in primates (H3-H6, M. Hefford, unpubl BSc dissertation, University of Bath, 2019).

### **Reptiles, Amphibians and Fishes**

- We collected ASR data for amphibians and reptiles from more than 210 species, and although these datasets are not yet comparable to birds, we used these data for several analyses (Vági et al. 2019 Proc Roy Soc B, Pipoly et al. in prep).
- Using over 1000 species of frogs and toads, we analysed the diversity of parental care in frogs (see H6) and showed that terrestrial breeding habitat is the best predictor of complex parenting

(Vági et al. 2019 Proc Roy Soc B). We also analysed the associations between ASR, ambient environment and frog parental care (H6). Results suggest that ASR does not predict parental care in frogs (Vági et al. 2019 Global Ecology & Biogeography). The latter publication is focused on the social and abiotic predictors of parental care diversity, along with Dr Vági's postdoctoral project (NKFIH: PD 132819).

- Bókonyi et al. (2019 BMC Evol Biol) demonstrated that sex difference in maturation age (bimaturism) is associated with ASR variation in reptiles (see H1–H3).
- We assembled a database on reptile parental care, ASR and life histories to address H1-H3 & H6, and run analyses to investigate whether ASR predicts parental behaviour and/or mating system variation. We showed that ASR is related to multiple paternity in reptiles (H5), as multiple paternity is more common when ASR is male-biased. Currently we are drafting the manuscript based on these results, and preparing for publication (Pipoly et al, in prep).
- We collated life-history and reproduction data from ray-finned fishes (Actinopterygii) with the objective of extracting ASR data from the published literature. However, reliable ASR data are scarce in the literature, therefore we decided to re-focus the latter project on phylogenetic analyses of parental care (Katona et al. in prep).

### Reviews and Commentary

- We edited a special issue for the journal Philosophical Transactions of the Royal Society with 16 papers about ASR evolution (Schacht, Kramer, Székely & Kappeler (eds). 2017. Adult sex ratios and reproductive decisions: a critical re-examination of sex differences in human and animal societies).
- We investigated the relationship between the intensity of sexual selection (as indicated by body size dimorphism) and ASR (H4 & H5). Results consistently show that SSD in birds and mammals is predicted by ASR, although this relationship, intriguingly, is the opposite of the one expected by most research workers in the field of sexual selection (including Charles Darwin) since we are finding that intense sexual selection appears to be related to female-biased ASR (Liker et al. in prep).
- Experimental manipulations of ASR are scarce in wild populations, and we were invited by the editor of Current Biology to comment a recent experimental manipulation of ASR in a nuthatch population (Kingma and Székely 2019).

### Career development

- The ASR project also supported career progression. The experience of the post-doctoral researcher, Dr Vági, employed on the project led to a successful fellowship application. Dr Vági is pursuing independent research career although he continues collaborating with the PIs of the ASR project (Profs Székely, Liker & Freckleton).
- In 2020 Dr Ivett Pipoly (MTA-PE Evolutionary Ecology Research Group, University of Pannonia) joined the ASR project as a postdoctoral researcher and contributed to the bird and mammal research. She is now working on four research topics emerged from this ASR NKFIH project, and she is planning to apply for a NKFIH PD\_21 grant.
- Gergely Katona and Karola Szemán started their PhD at University of Debrecen on topics related to the ASR project. They completed 4 and 3 years of their PhD education, respectively. As most of their research achievements are submitted for publication, they are close to completing the PhD. They played a significant role in data collection, supervision of undergraduates and the group's social life organization.
- Several undergraduates (including students from the University of Bath, UK on placements at University of Debrecen) joined in the ASR project and contributed by collecting data from fishes, amphibians, reptiles, birds and mammals. Thanks to the coordinated efforts of these students in

which Dr Vági played a key role, we have now a good amount of data on ASR, life history, social behaviour and demography from nearly all major vertebrate groups.

### **International and national cooperations**

- The backbone of the ASR project was the collaboration between University of Debrecen (Prof Székely), University of Pannonia (Prof Liker) and Sheffield University (Prof Freckleton). In addition, for specific skills and expertise, we cooperated with leading research scientists including Prof Jean-Michel Gaillard (CNRS, Lyon), Dr Jean-François Lemaître (CNRS, Lyon), Dr Daniel Field (University of Cambridge), Dr Zsolt Végvári (Centre for Ecology, Budapest) and Dr Veronika Bókonyi (Plant Protection Institute, Budapest).

### **Invited research seminars**

We were invited to present the results of the ASR project at several universities and research institutions that included:

- 2020 Universities for Science Consortium, Mexico, online presentation
- 2019 Eötvös University, Fruits of Ethology; Department of Biology, University of Copenhagen (Denmark); Faculty of Life-Sciences, Beijing Normal University (China); Shenzhen Ornithological Society (China); 70th anniversary of Science Faculty of University of Debrecen
- 2018 Cardiff University (UK), Beijing Normal University, Sun Yat-sen University (China)
- 2017 Max Planck Institute for Evolutionary Anthropology, Leipzig (Germany); University of Santiago de Compostela (Spain), Gubelkian Research Institute (Portugal), University of Stockholm (Sweden), Beijing Normal University (China), Department of Life Sciences, University of Groningen (Netherlands)
- 2016 Centre for Social Evolution, University Copenhagen (Denmark); Dept of Life Sciences, University of Groningen; International Institute for Applied Systems Analysis, Laxenburg (Austria); Dept of Ecology & Systematics, Eötvös University, Budapest.

### **Workshops, conferences**

- Our team organised one ASR workshop (Debrecen in April 2016), and three international symposia (Adult sex ratios and reproductive strategies: Berlin February 2017; Sex roles and sex ratios: Tihany, April 2017; Reproductive strategies: Debrecen, November 2019): these events were well attended by students and scientists from Hungary and internationally. The ASR team presented results in all of these events.
- Every year we participated at the Hungarian Ethologists Conference with multiple presentations.
- We presented our results at two international conferences of the European Society of Evolutionary Biology (ESEB; Groningen 2017; Turku 2019)
- We had presentations at the annual meetings of ÉLVONAL-funded research Conferences (Hortobágy 2017; Debrecen 2018)
- We also presented our results at Hungarian Ethologists Conference, Kolozsvár/Cluj (2018) and at the Hungarian Herpetology Symposium (Budapest 2019)
- Invited conference / workshop presentation included:
  - Biological bases of behaviour, 25th anniversary of Tlaxcala Postgraduate Workshop, Mexico, 26-30 October 2020, online
  - Sex difference in life expectancy, Workshop organised by Max Planck Research Group in Demography, Odense, Denmark; July 2019
  - International Ornithological Conference, Vancouver (Canada), August 2018, invited symposium keynote speaker
  - Genes, sex and behaviour Symposium, Mexico City, September 2018, invited speaker

- The use of ecology for the society. Hungarian Academy of Sciences, Budapest, November 2017
- Legacy of Miklos Udvardy, University of Debrecen, November 2017
- International Wader Study Group Conference, September 2017, Prague, invited plenary speaker
- European Neuroscience Conference, September 2017, Pécs, invited symposium speaker
- Workshop on adult sex ratios and reproductive decisions, Berlin, February 2017, invited speaker
- Evolution of sex roles workshop, April 2017, Tihany, invited speaker
- Model systems in animal behaviour, Hungarian Ethologists Conference, 2-4 December 2016, Debrecen, plenary speaker
- First conference of B10k consortium, 26-29 October, Beijing, China, invited speaker
- Science and Humanities Conference of Mexican Academy of Sciences, 24-26 August, Mexico City, invited speaker

## Publicity and outreach

- Our team was involved in various public events and/or presentations to a wide audience including the Udvardy Miklós Symposium (Debrecen; Online Biology Conference); at the annual Researchers' Nights at University of Debrecen
- Our works have been well covered by press releases. For instance, the press release on Lemaitre et al. (2020 PNAS) has been highlighted by 44 national and international newspapers, magazines and online media including BBC, National Geographic, The Times, The Guardian and ScienceDaily. The estimated total news reach was 129 million people.



## Publications emerged from the project

Ancona, S., A. Liker, M. C. Carmona-Isunza & T. Székely.: **Sex differences in age-to-maturation relate to sexual selection and adult sex ratios in birds**, *Evolution Letters* 4: 44-53, 2019

Ancona, S., F. V. Dénes, O. Krüger, T. Székely & S. R. Beissinger: **Estimating adult sex ratios in nature**, *Philosophical Transactions of The Royal Society* 372: 20160313, 2017

Bókony, V., G. Milne, I. Pipoly, T. Székely & A. Liker: **Sex ratios and bimaturism differ between temperature-dependent and genetic sex determination systems in reptiles.**, *BMC Evolutionary Biology* 19:57, 2019

Bókony, V., S. Kövér, E. Nemesvázi, A. Liker & T. Székely: **Climate-driven shifts in sex ratios via sex reversals in ectotherms with genetic sex determination**, *Philosophical Transactions of The Royal Society* 372: 20160325, 2017

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- Kingma, S, T. Székely: **Social behaviour: males help when mates are rare**, Current Biology 29: R358 -R380, 2019
- Komdeur, J., T. Székely, X. Long & S. A. Kingma: **Adult sex ratios and their implications for cooperative breeding**, Philosophical Transactions of The Royal Society 372: 20160322, 2017
- Lemaitre JF, Ronget V, Tidiere M, Allainé D, Berger V, Cohas A, Colchero F, Conde DA, Garratt M, Liker A, Marais GAB, Scheuerlein A, Székely T, Gaillard JM: **Sex differences in adult lifespan and aging rates of mortality across wild mammals**. Proc Nat Acad Sci USA 117: 8546-8553, 2020
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