



THE SIGNIFICANCE OF ADULT SEX
RATIOS: FROM POPULATIONS TO
PHYLOGENIES
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I am an evolutionary biologist interested in social behaviour who has published over 280 peer-reviewed articles and four books. I combine different tools and approaches to understand evolution, working from genes and genomes to individuals and populations. A researcher and university teacher, I have supervised 28 Ph.D. students and mentored 14 post-docs and research fellows; the vast majority are employed in academia or research as professors or independent investigators. I was a Visiting Professor at Harvard University and the Universities of Groningen, Bielefeld and Göttingen and am a Distinguished Professor at Sun Yat-Sen University (China) and the University of Debrecen (Hungary). I received a Humboldt Award and currently am a Royal Society Wolfson Research Merit Award Holder. My current research focuses on two themes: 1. the evolution of mating systems, parental care and sex roles and 2. we are recently discovering that an overlooked component of social systems (and of breeding system variation) is adult sex ratio. I am a dedicated conservation biologist and founded an award-winning conservation NGO in West Africa in 2010 and have served the NGO as President ever since. – Address: Department of Biology and Biochemistry, University of Bath, 4 South 0.26, Bath, BA2 7AY, United Kingdom. E-mail: t.szekely@bath.ac.uk.

Adult sex ratios are highly variable between organisms: some animals have only females in their population, whereas others have more males than females. How does this variation emerge? And why are these variations important? Understanding the causes and implications of adult sex ratio variation is important for both human and non-human societies.

In this Wiko Focus Group, we address adult sex ratio (ASR), which is usually quantified as the proportion of males in the adult population.

My Wiko project had two specific objectives. First, to establish what causes ASR variation in mammals, birds, reptiles, amphibians and fishes. Second, to explore how ASR variation is related to variation across species (or populations) in mating systems and parental care. My overarching objective was to find broad-scale patterns that cut across the many millions of years of independent vertebrate evolution in these five groups.

I made substantial progress toward achieving these objectives.

1. Workshop. As part of the activities of this year's Wiko Focus Group on *Causes and Implications of Adult Sex Ratio Variation in Vertebrates*, we organised a workshop on adult sex ratios and reproductive decisions on February 2–3, 2017 at the Wissenschaftskolleg. The workshop was attended by 30 delegates, 14 of whom contributed a paper. Parts of the workshop were also attended by other Wiko Fellows.

The insight that reproductive decisions of humans and animals are often influenced by variation in the number of adult males and females present in a given population is a fairly recent one. Two more or less independent strands of inquiry in the social and biological sciences had investigated the relationship between variation in adult sex ratios and behavioural components of sex roles. Interestingly, social science studies in this field always had a strong applied aspect, whereas biology devoted much more effort to theory development and modelling.

The workshop at Wiko was truly remarkable because it was the first time that biologists and social scientists working on this topic came together for exchange and discussion. The workshop tackled both evolutionary and social science aspects of sex ratio variation, and it initiated a dialogue between scientists using a variety of approaches and different model systems to understand sex ratio variation. Finding a common language or currency is often the main obstacle to interdisciplinary collaboration. At this workshop, we managed to circumvent many of these usual obstacles, for example by agreeing on using the same metric for quantifying ASR variation in our analyses, which will greatly facilitate comparisons across species and study systems

2. Theme Issue of the Philosophical Transactions of the Royal Society (Series B). Based on the workshop, two members of the Focus Group (Kappeler and Székely) teamed up with two social scientists (Kramer and Schacht) to jointly write an introductory review on the topic.

Because the oral contributions to the workshop will be published as a Theme Issue, the interdisciplinary discourse at the workshop will have lasting impact on the field, also beyond the future work of the actual participants, not least because we also identified important open questions for future research on the causes and consequences of sex ratio variation.

The Theme Issue included 16 review publications by leading scientists in their fields and was published on September 19, 2017. I contributed to four review papers in the Theme Issue (see below).

3. *Wiko Colloquium*. The Wiko project provided an excellent opportunity to summarise my personal research – much of it focused on sex ratios. In my Wiko colloquium, I explained the rationale, which had the following main elements.

The story started in 1990, when I realised that in my favourite study species, the Kentish plover – a small shorebird that has fascinating mating and parenting behaviour – one parent abandons the family: usually the female leaves her mate and the offspring. Why do females abandon the family? The answer seems to lie in the harsh world of natural selection: females abandon their family to seek a new mate and to increase their reproductive success – i.e. to enhance their Darwinian fitness – even though this is bad for their mate, since their mate may spend a month rearing the young to independence, and whilst he alone looks after the young he can be killed by a predator.

But why do females abandon the family more often than males do? The answer, I suspected, lies in the adult sex ratio. If a population has many bachelor males, the females' chances of remating are favoured, so they are more likely to remate and reneest than the males are. To investigate these propositions, we carried out an experiment in the natural habitat of plovers to quantify the time it takes for unmated males and females to find a new partner and reproduce. In addition, we also modelled the number of males and females in the population using demographic analyses: both the field experiment and the demographic analyses showed that, indeed, in the Kentish plover population there are lot more males than females.

How general are these results? To test the generality of the relationship between mating system and adult sex ratio, we used one of the oldest approaches in biology – the comparative approach. Biologists ever since Aristotle are aware of the importance of cross-species comparisons, although in the last 30 years these techniques have changed fundamentally. The key idea here is that by using phylogenies, one can test whether the associations between ASR, mating and parenting hold across a broad range of taxa.

Indeed, using phylogenetic comparisons, we showed there are strong relationships between mating, parenting and ASR not only in shorebirds – the group of organisms that include plovers – but also across birds as a whole.

4. *Spin-offs*. The Wiko provided excellent opportunities to accelerate my research that led to numerous publications. I wish to highlight here two specific pieces of work that were carried out in collaboration with scientists based at Bielefeld University. In one of these papers (Eberhart-Phillips et al. 2017), we developed a new demographic model to estimate adult sex ratio. Using this model and detailed data from a well-studied plover population, we estimated a highly male-biased ASR. Using the new model, we were also able to disentangle which stage of life-history made the strongest impact on ASR.

In the other paper (Eberhart-Phillips et al., in review), we used the aforementioned modelling approach for six different plover populations. Using detailed information from these populations, we showed that some of these populations exhibit male-biased ASR, whereas others were evenly divided or were female-biased. Importantly, ASR variation predicted the extent of parental cooperation, since in populations with even ASR both parents cooperate to rear the young, whereas in populations with skewed ASR only one parent reared the young. The latter result suggests that there might be a causal relationship between the extent of ASR bias and parental care variation.

Taken together, the Wiko project was highly successful and led to numerous high-profile publications. Whilst the main thrust of these publications was adult sex ratio, my work impacted on other areas of evolutionary biology and biodiversity conservation. I would like to thank all Wiko staff for their immense support and understanding, which made my stay not only productive, but also highly enjoyable.

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