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REVIEW

Evolution of reproductive strategies: sex roles, sex ratios and phylogenies

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Abstract
Behavioural variations associated with breeding—termed reproductive strategies—are some of the striking behaviours that have occupied naturalists for 1000s of years. How an animal seeks, competes for and/or chooses a mate? Do they breed with a single partner, or do they change partners between breeding events? How and when do they look after their young? Behavioural biologists, ecologists and evolutionary biologists have investigated these questions using quantitative methods since 1970s. In Debrecen, with the support and mentoring of Prof Zoltán Varga, we are investigating the causes and implications of reproductive strategies since 1988. This article reviews some of the core ideas in reproductive strategies research and explains the influence of Prof Varga on the development of these ideas. My main thesis here is that both integrative thinking and adopting a multi-pronged research approach using an explicit phylogenetic framework—both of these have been spearheaded by Prof Varga throughout his lifetime—can reveal novel aspects of reproductive strategies. Importantly, some of these academic insights have direct implications for preserving species and their habitats in the wild, and thus benefit biodiversity conservation.

Keywords Reproduction · Mate choice · Mating systems · Parental care · Adult sex ratio · Population demography · Phylogenetic comparative analyses · Biodiversity

Introduction

All started in Debrecen in late 1980s. Reproductive strategy was an emerging topic in behavioural ecology with exciting discoveries showing diverse mating behaviour and mate choice among insects, birds and mammals. To develop these new ideas—that were already becoming mainstream biology in the USA, Great Britain and Sweden—in 1989 we organised an informal meeting at Kossuth University, which later became the University of Debrecen (Fig. 1). The small but enthusiastic core of this workshop went ahead and established the Behavioural Ecology Research Group, i.e. VÖCS, as it became known from the Hungarian acronym of the Viselkedésökológiai Kutatócsoport. Prof Varga—the head of Department of Zoology at Kossuth University at that time—was quick to realise the potential in studies of behavioural ecology, and he supported wholeheartedly both the workshop and the new research group.

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Why study plovers?

This was the time I started to work on shorebirds. After spending a year at the Edward Grey Institute at Oxford—one of the hotbeds of behavioural ecology—I became interested in mating systems and parental behaviour. I choose to investigate a small drab shorebird, the Kentish plover *Charadrius alexandrinus* in Southern Hungary where they were reasonably common breeding birds of alkaline grasslands. My main objective was to understand their breeding behaviour using individually marked birds. Colour ringing of wild birds for individual identification had just started at that time in Hungary, and by using individual recognition, we were hoping

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Fig. 1 Participants of the workshop on reproductive strategies in Debrecen, 1989. Members of VÖCS (Behavioural Ecology Research Group; back row, starting at the third person from left: Szabolcs Lengyel, Gábor Noszály, Tibor Fuisz, Zoltán Barta, Hédi Mező, István Karsai, Tamás Székely, Tibor Szép, András Liker)

to learn about movements, repeated nesting attempts and mate changes—and ultimately, reproductive success—of adult birds in order to test predictions of life history theory (cost of reproduction), ecology (habitat use) and site fidelity (Székely 1992; Székely and Lessells 1993). These works run parallel with the research of an excellent behavioural ecology team at Eötvös Loránd University (Budapest) that is focused on passerine life history decisions (Török and Ludvig 1988; Török and Tóth 1988).

Kentish plovers are a great system to work with (Fig. 2 left, Székely 2019). They nest on the ground so I was able to access their nests, trap both the parents and their chicks at their nest. Also, they breed in open habitats so that the adults and their chicks can be observed, and using individual combination of colour rings the behaviour and local movements of individuals can be monitored. Plovers are also tame and trusty—in places like Southern Hungary (Szeged, Kistelek, Pusztaszer and nearby) they were habituated to people and livestock such as sheep flocks grazing around their nests—so plovers readily accepted the presence of an observer. Some of the first patterns I noticed was that one parent (more often the female parent) left the family so that the male parent alone reared the chicks to independence (Fig. 2 middle). I also noticed that individual plovers (and also, pairs), moved between different sites in search of new breeding habitats (Fig. 2 right). These two patterns (i.e. brood care and movements of divorced plovers) seemed initially independent from each other, and it took me decades to work out that they are in fact, tightly related (see below).

My initial toolkit included only behavioural observations, although from early 1990s I increasingly used experiments in the field following the prevailing mantra in behavioural ecology at that time, i.e. *to test a hypothesis properly, one needs to interfere with the natural reproduction and use experimental manipulation*, since observational data are inherently correlational and hence the causes, the consequences, and the latent effects are nearly impossible to separate using only observations. The advocacy for field experiments emerged from the legacy of Niko Tinbergen who became famous for his elegant field manipulations of wasps, gulls and shorebirds and was

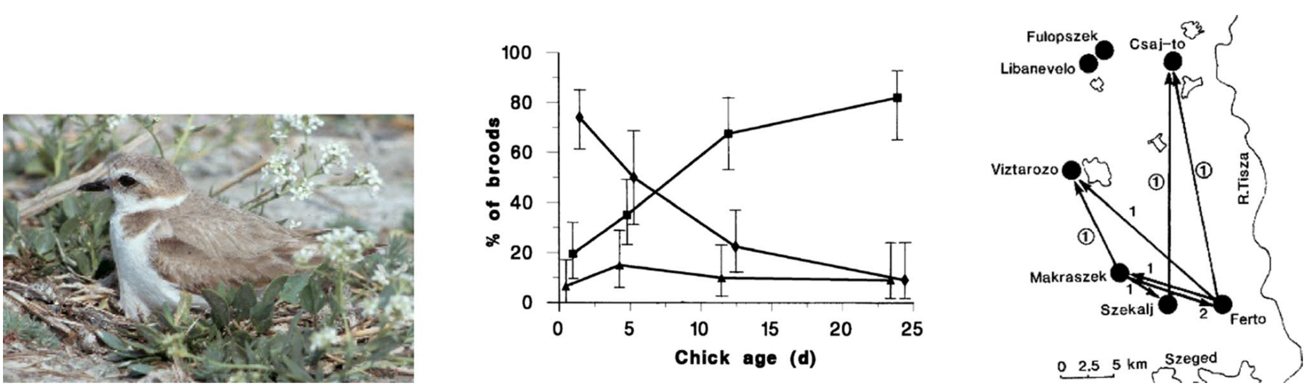

Fig. 2 Female Kentish plover on her nest (left, © Gábor Lendvai), brood care pattern in relation to chick age (middle) and movement of Kentish plover pairs (right, uncircled numbers) and divorced individuals (circled numbers) in Southern Hungary (Székely & Lessells 1993)

based at Oxford much of his active life (Krebs and Davies 1978; Dawkins et al. 1991).

Whilst the scientific value of a well-designed manipulative experiment is undeniable, the values of observational studies—especially in the context of long-term monitoring of wild populations—are vindicated more recently (Clutton-Brock and Sheldon 2010; De Villemereuil et al. 2020). Long-term data are valuable because they can reveal how consistent a given animal is in a particular situation, and these can lead to estimating evolutionary changes in the population using quantitative genetic theories. In addition, long-term studies can reveal changes and fluctuations in demography, behaviour and ecology (Grant and Grant 2019), and these temporal variations are increasingly important for understanding resilience and responses of wild populations to natural and human-induced stressors (Capdevila et al. 2020; Kubelka et al. 2022).

Sex roles

My research initially focused on parental care, although over time it expanded into mating systems, pair bonds and habitat selection (Székely 1992; Blomqvist et al. 2002) and more recently, into sex roles, i.e. behavioural differences between males and females in the context of reproduction (Mokos et al. 2021; Gonzalez-Voyer et al. 2022).

Whilst parenting behaviour at that time (and to some extent, still today) is investigated largely in isolation from the rest of reproduction (Mock 2022), my research team quickly realised that to understand parenting in plovers, we also need to know the future of the parents, i.e. whether they can find a new mate and breed successfully, i.e. the mating opportunities. The interactions between mate search, pair bonding and parenting came out from a series of game-theoretic models that were developed with bright theoreticians (McNamara et al. 2000; Houston et al. 2005; Barta et al. 2014), and we popularised the idea in a publication that emerged from a workshop in Erice (Italy) in 1998 (Fig. 3, Székely et al. 2000). The theory-driven insights of mutual dependence between pair bonding, mating opportunities and parenting are one of the main pillars of my research ever since (Gonzalez-Voyer et al. 2022; Schacht et al. 2022; McDonald et al. 2023)—these insights were driven by both the natural behaviour of plovers (Fig. 2) and mathematical theory (Fig. 3).

Sex ratios

Parallel with studies of parenting and mate fidelity in Kentish plover, I became interested in sex ratios following the insightful suggestion of Kate Lessells who suspected that a neglected aspect of reproductive strategies in

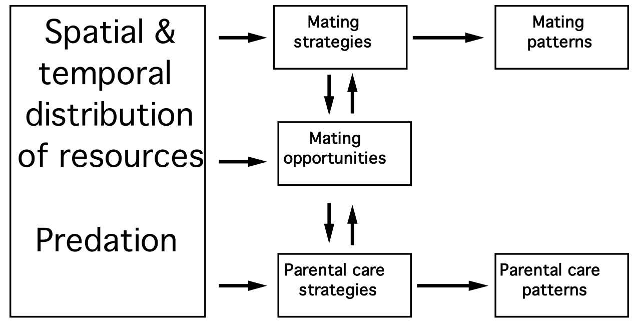

Fig. 3 The interdependence of mating behaviour, mating opportunities and parental care (reproduced from Székely et al. 2000)

multiple-breeding organisms is mating opportunity. A single population of Kentish plover may exhibit social monogamy, polyandry and polygyny, and at the same time, the chicks can be reared by both parents, the male parent alone or the female parent alone (Lessells 1984). It was striking that in several plover populations, the female parent abandoned the family (Lessells 1984; Warriner et al. 1986; Székely and Lessells 1993; Amat et al. 1999)—that seemed to go against the prevailing evolutionary mantra that the females are selected to look after the young especially in internally fertilising species such as reptiles, birds and mammals for two reasons: the male is uncertain since females could copulate with multiple partners whereas the female is somehow "predisposed" to look after the eggs or young given the offspring is developing in her body (Trivers 1972; Kokko and Jennions 2008). A possible—but difficult—explanation to test in the field was that different mating opportunities for males and females may drive brood care patterns since the number of males and females in a breeding population may not be even. For Kentish plovers, the expectation was that for females the mating opportunities were better than for males and an obvious reason for this bias would be male-skewed adult sex ratio (Kosztolányi et al. 2011). I am glad that at that time I was not blinded by Fisher's frequency-dependent sex allocation argument that would supposedly produce even adult sex ratios (i.e. 50 males : 50 females) in wild dioecious populations (Fisher 1930; Trivers 1985). Thus, I piously started to record the number of adult male and female Kentish plovers throughout the breeding season to give clues about mating opportunities for males and females. By watching plovers in the field and talking to a fellow plover biologist (Paul Jönsson) who investigated a small breeding population in Sweden, I became convinced that Kentish plovers have male-skewed adult sex ratios, at least in these well-marked populations (Jönsson 1993).

With hindsight, simply counting males and females in the field is doomed to failure for at least two reasons. First, there are always a number of unmarked birds so for these birds it is difficult to establish whether they are all different individuals. Also, unmarked birds can move around and thus can confuse the headcounts. Second, males and females often have different daily routines and/or habitat preferences, and thus, simply counting the visible individuals may well be biased. For instance, if females incubating the nests during daytime whereas the males incubate the eggs at night—a pattern that occurs in several plovers (AlRashidi et al. 2011; Vincze et al. 2013), the observer bound to spot more males during the day than females—a bias which may not reflect the true number of adults in an area.

To overcome the limitation of count-based adult sex ratio (ASR), we used a two-pronged approach. First, in a large breeding population of Kentish plovers in Tuzla (Turkey) we experimentally created unpaired males and unpaired females by removing their mate, and recorded the time they took to find a new mate and renest. As predicted by the male-biased parenting observed in several plover populations (Warriner et al. 1986, Székely and Lessells 1993; Amat et al. 1999; Kosztolányi et al. 2006), the experimentally unpaired females usually found a new mate in less than one day, whereas the unpaired males took usually over 10 days to find a new mate, if they found a new mate at all (Székely et al. 1999).

Second, by establishing the sex of hatchling plovers in the nest and by estimating the sex-specific survival of male and female plovers from hatch till adulthood, we developed a demographic model using data from Tuzla (Kosztolányi et al. 2011). Using the latter protocol, we estimated that an astonishing 6.1 times more males were in the population than females. Reassuringly, the experimental-based ASR and the demography-based ASR estimates were in the same ballpark region, and importantly, both suggested a heavily male-skewed ASR. A follow-up demographic study using more advanced modelling confirmed the male-skewed ASR in some (but not all) plover populations (Eberhart-Phillips et al. 2017).

Why phylogeny matters?

Parallel with a boom in field studies of fishes, birds and mammals in early 1970s summarised by inspirational books on sociobiology (Wilson 1975)—or as it was called in this side of Atlantic, behavioural ecology (Krebs and Davies 1978)—there was another revolution in studies of animal behaviour: comparative analyses. This approach goes back to the pioneering works of Niko Tinbergen on gulls (Dawkins et al. 1991) and James Crook on weaverbirds (Crook 1964), and was synthesised by a stimulating book on ecological adaptations for breeding by David Lack—the director of Edward Grey Institute in Oxford (Lack 1968). With the emergence of wealth of data on natural history, new statistical approaches have been proposed to compare species and populations across the phylogeny (Felsenstein 1985; Harvey and Pagel 1991). Phylogenetic comparative analyses were further stimulated by the rapid developments in inferring phylogenetic relationships among extant taxa (the "tree of life") using molecular data. The comparative method as it became known was attractive for me having been primed to phylogenetic analyses by Zoltán Varga's lectures on phylogeography, speciation and behaviour at Kossuth University (Varga 1981).

Using the comparative approach, we initially inferred the history and ecological predictors of parental care in shorebirds (Székely and Reynolds 1995; Reynolds and Székely 1997), and then branched out to tackle parental care across birds (Gonzalez-Voyer et al. 2022; Long et al. 2022). Most recently, we expanded the approach to reproductive strategies and social organisation of bony fishes, sharks and rays, salamanders, frogs and toads, reptiles and mammals (Katona et al. 2023, Vági et al. 2019; Szemán et al. 2021; Song et al. 2022; Pipoly et al. 2023). Together, these studies produced two major insights. First, it appears that different components of reproductive strategies may co-evolve together although the phylogenetic associations between these different components may vary between clades (Gonzalez-Voyer et al. 2022, Székely et al. in review). This is important, since it implies that to understand mate choice in a given organisms, we also need to know their pair-bond strategies and parenting as well. Second, the fertilisation mode in ectotherms (i.e. external/internal fertilisation) and the adult sex ratio in endotherms (i.e. male-skewed ASR/female-skewed ASR) are emerging as major predictors of reproductive strategies in vertebrates (Liker et al. 2014; Gonzalez-Voyer et al. 2022; Schacht et al. 2022). Importantly, the phylogenetic comparative analyses across birds somehow mirror the field-based discoveries we made in plovers (see above), specifically in that male-biased parenting appears to be associated with male-skewed ASR supporting the argument that males stay with the offspring more likely than the female if he has limited opportunities to breed with a new partner (Kosztolányi et al. 2011; Liker et al. 2014). However, whether the associations between reproductive strategies and ASR may also occur in non-avian systems will need to be investigated.

Comparative studies can expand the scope of field-based research and put ecological/behavioural processes and patterns into a broader phylogenetic perspective. For instance, a popular idea emerging from studies of reproductive strategies that much of the difference between male and female reproduction originates in the size differences between the gametes, termed anisogamy (Parker et al. 1972). Anisogamy is common across the animal kingdom since males tend to produce many small games, whereas the female gametes are nutritious but far and few. The inequality in number and sizes of gametes are assumed to drive more intense sexual selection among males than among females and have knock on consequences for the “typical” reproductive strategies of males and females (Janicke et al. 2016). Whilst this scenario, often labelled as the Darwin–Bateman paradigm, has a lot of support, an element of this scenario is controversial (Fig. 4) since the extent of anisogamy did not predict the differential selections acting on males and females (Mokos et al. 2021). Importantly, however, parental behaviour does seem to predict the intensity of sexual selection acting on males relative to females—at least in those organisms that exhibit some level of care—suggesting that rather than anisogamy per se, parenting is the one that might be associated with sexual selection (Fig. 4). Disentangling the causes, the consequences and the various feedbacks are some of the toughest tasks in biology (Carroll 2016), although using a multi-pronged approach we can now deal with these challenges to advance the evolutionary understanding of sex differences and sex roles.

Conclusions

Prof Zoltán Varga’s scientific approach and insights have influenced my research in several important ways, beyond simply mentoring myself and other younger colleagues interested in evolution, phylogeography, ecology and behaviour. First, Zoltán always emphasised the importance of integrative thinking. Whilst science is increasingly reductionist and tends to force us into a small mental cage within which we are trying to find solution—an approach captured by the quote credited to Abraham Maslow: “*If your only tool is a hammer then every problem looks like a nail*”. Zoltán, in contrast, is an integrative thinker and he dares to venture into distant research fields to find an answer to seemingly disjunct facts.

Second, I benefitted from the insightful discussions with Zoltán about the roles of phylogeny in evolution. There is always a temptation to view an organism as it behaves in a laboratory or in a field as a response to current adaptive factors, although we should bear in mind that these organisms (including humans too), are the descendants of thousands of generations that had to cope with their past environments. No biologist should ignore phylogenies—indeed, they are in our genes (Quammen 2018).

Third, Zoltán spent much of his lifetime on discovering new species, and finding out how populations diversify and new species emerge (Varga 2008, 2019). The combination of evolutionary systematics and phylogeography left long-lasting effect on my work: we identified cryptic plover species (e.g. snowy plover *Charadrius nivosus*, Küpper et al. 2009, white-faced plover *Charadrius dealbatus* Wang et al. 2019). To understand speciation, our team is also exploring a link between sex roles and speciation by suggesting that in polygamous birds there is weaker geographic differentiation between populations due to the extensive movements of adults whilst they are searching for a new mate (Fig. 2, D’Urban Jackson et al. 2017).

Finally, beyond fundamental evolutionary research, Zoltan’s lifetime achievements include a huge amount of conservation-related works (Kocsis et al. 2018; Varga 2019). By setting these examples including the long-term butterfly and moth monitoring network in Aggtelek National Park, Hungary, he inspires the younger generation including myself to take biodiversity conservation seriously and seek to use the evolutionary approach to benefit wildlife. A spin-off of our approach was a designation of a new RAMSAR site the Salinas Porto Ingles in Cape Verde (Oliveira 2013)—a saltmarsh where we continue to investigate Kentish plovers since 2007. Also, the very study site where much of the early research into reproductive strategies of shorebirds took place (Lendvai and Székely 1994; Lengyel 1996; Liker 1998), is now the location where a team of zoologists, botanists and conservationists are aiming to reconstruct the rich

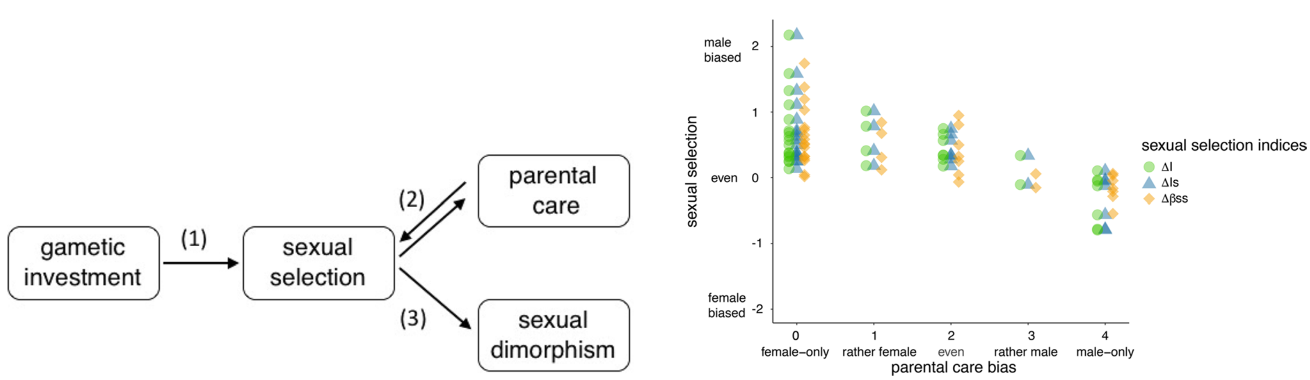

Fig. 4 The hypothesised associations between the extent of anisogamy (labelled as gametic investment), sexual selection, parental care and sexual size dimorphism (left, Janicke et al. 2016). Stronger sexual selection on males associates with female-biased parental care and vice versa (right, Mokos et al. 2021). The intensity of sexual selection is indicated by three indices: Δ*I* (opportunity of selection), ΔIs (opportunity for sexual selection) and Δβss (Bateman gradient) in relation to sex-biased parental care ($N=37$ species)

grassland bird community that has disappeared from there (LIFE 2020).

Acknowledgements This short review touches upon some of the conceptual insights I gained from working with Prof Zoltán Varga. I also appreciate his relentless support towards myself and my research group. The research mentioned in this review benefitted from contributions by a team of field assistants, students, postdoctoral researchers and collaborators: see the Acknowledgements of specific papers. Funding was provided by the National Research and Innovation Office of Hungary (ÉLVONAL KKP-126949), Eötvös Loránd Research Network (Ref 1102207), the Royal Society (Wolfson Merit Award WM170050) and various other funders—see their details in specific publications. I very appreciate the insightful comments and suggestions of Gábor Sramkó, Grant C. McDonald and two anonymous reviewers.

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