



Editorial: The Development and Fitness Consequences of Sex Roles

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Editorial on the Research Topic

The Development and Fitness Consequences of Sex Roles

INTRODUCTION

In most sexually reproducing species, males and females are characterised by differences in reproductive behaviours and life-history strategy (Kokko et al., 2006; Fairbairn, 2013). Exploring the origin and consequences of sex roles are key questions in evolutionary biology, yet we are far from understanding their developmental mechanisms and adaptive significance. We aim to highlight this research field and broaden the range of taxa and phenomena investigated in relation to sex roles.

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SEX-SPECIFIC LIFE HISTORIES, SEX RATIOS, AND SEX REVERSAL

A major driver of the evolution of sex roles is adult sex ratio (Liker et al., 2013; Kappeler, 2017). Avian studies suggested sex-ratio variation to stem from sex differences in juvenile and adult mortality, and maturation times (Székely et al., 2014; Ancona et al., 2020). Recently, however, a more complex picture developed, emphasising early-life processes and environmental effects, which proved to be a popular subject in the Research Topic with three articles. Furthermore, sex-specific life-history strategies can influence the time and probability of dispersal from the natal territory (Emlen, 1982; Li and Kokko, 2019), or the adjustment of parental investment in response to the partner's effort in biparental species (Houston et al., 2005); two further research papers focus on these strategic questions in our collection.

Nusbaumer et al. investigate expression of sex-specific life-history in early life stages. In a stressful, polluted environment, female lake char (*Salvelinus umbla*) hatch later and are more likely to die than male embryos, indicating faster growth rates and higher resistance to pollution in males during embryo development. This implies that sex-specific life-history strategies, population sex ratios and divergent sex roles can be a result of environmental challenges impacting the earliest life stages.

Lambert et al. investigate the relative importance of sex-specific larval mortality and sex reversal in green frogs (*Rana clamitans*). With advancing stages, the genetic sex ratios shift towards females, implying male-biased mortality. Sex reversal in both directions also contributes to the phenotypic

sex ratios at metamorphosis. Female-to-male sex reversal is the highest in the pond with the most acidic pH and lowest dissolved oxygen levels. Although the effects are small, they suggest that population sex ratios may be influenced by early-life sex differences in survival and sex reversal due to environmental stressors.

In agile frogs (*Rana dalmatina*), another species with sex reversal, Bókonyi et al. investigate whether sex reversal is associated with life-history and early behavioural differences. Of 16 variables related to growth, development, larval foraging, and risk-taking behaviours, they find only a few differences between spontaneously sex-reversed and sex-concordant individuals, with no consistent support for either higher or lower fitness prospects to sex-reversed individuals. In light of their earlier findings on reduced fitness when sex reversal was triggered by heat stress, they formulate a new hypothesis that the fitness consequences of sex reversal may depend on its aetiology.

Josi et al. investigate the costs and benefits associated with sex- and life-history- specific dispersal in the cooperatively breeding cichlid *Neolamprologus savoryi*. Focusing on growth rates and survival, they identify distinct sex-specific routes to independent breeding. The study concludes that differences in dispersal decisions between and within the sexes are tightly linked to divergent life-history trajectories, including different growth rates, the age at obtaining breeder status, and survival.

Wang et al. investigate in burying beetles (*Nicrophorus vespilloides*) how parents change their effort and trade-off current and future reproductive investments when parental effort by their mate and brood reproductive value change simultaneously. They show that males compensate for loss of female care regardless of brood size, and this negatively affects their subsequent parental investment. Female compensation, however, depends on brood size, with compensation only at small broods. These findings suggest sex differences in the adjustment of reproductive allocation and sex-dependent reproductive trade-offs between current and future reproduction.

BREEDING SYSTEM AND PARENTAL SEX ROLES

Providing care, especially food provisioning, is among the most important and costly contributions of parents to realise and enhance fitness (Clutton-Brock, 1991; Kokko and Jennions, 2008; Royle et al., 2012). Three articles in our collection investigate the origin and consequences of parental sex role differences and their potential influence on breeding system evolution.

Fresneau et al. report their observations on courtship behaviour, mating competition, polygamy, and male-only care for offspring in pheasant-tailed jacobins (*Hydrophasianus chirurgus*), a species with sex-role reversal. While polyandry in females is close to the expected level (ca. 82%), males (with ca. 5% polygyny) perform more courtship displays and females participate partly in brood care. The study of Fresneau et al. is a useful contribution to understand the gradual evolution of sex-role reversal in this species and in general.

Ratz et al. using burying beetles (*Nicrophorus vespilloides*) as models, manipulate resource availability to investigate its potential role in the emergence of biparental care. They find that duration of male parental care is increased with more access to resources, whereas female care is independent of the manipulation. Thus, sex differences in parenting and the level of parental cooperation depends on environmental conditions.

Applying a full cross-fostering experimental design, Morvai et al. disentangle genetic and social parental effects in the ontogeny of parental sex roles in zebra finches (*Taeniopygia guttata*). By comparing incubation and offspring provisioning between the fostered second generation and the genetic/social parents, the authors report weak context-dependent genetic, social, and non-social environmental effects. They conclude the strongest and most consistent effect is the social effect by the current mate and highlight the importance of parental negotiation in explaining individual variation of parental sex roles in biparental species.

COGNITIVE MATE CHOICE IN VERTEBRATES

Selection on cognitive abilities might be different in the two sexes. Sex-specific behaviours may rely on cognitive skills to varying degrees, and mate choice and courtship behaviour may also involve cognition, contributing to sexual dimorphism in various cognitive abilities (Jacobs, 1996; Lindenfors et al., 2007). In a review paper, Fuss (a) provides support for the existence of cognitive sex differences, and the potential influence of cognition on mate choice decisions. The paper overviews evidence for context-dependent cognitive sex differences in mammals, birds, and fish. There is also strong evidence for cognitive abilities and learned elements in male display behaviours to influence individual mate choice decisions. Answering the question of how and to what extent individuals use their own cognitive skills to assess those of their prospective partners proves to be challenging. The author suggests methodological improvements for future test paradigms.

In another paper Fuss (b) reviews the neuronal prerequisites that support the triad of mate choice, sex roles and sexual cognition. Empirical research based on different methods reveal convincingly that the sex and the sex roles within the prevalent mating system are mirrored at neuronal levels in individual brain regions. Our knowledge so far relies on a confined set of networks and selection of brain regions. The author suggests behavioural studies should be combined with state-of-the-art neuroanatomical techniques to establish causal relationships and interactions between observed behavioural patterns and underlying mechanisms.

CONCLUSIONS

Contributions to this Research Topic reflect renewed interest and diversifying approaches to understand the ontogeny

and evolution of sex roles. Sex differences in life history and mortality in early ontogenetic stages are increasingly identified as important drivers of population sex ratios and thereby of sex roles, especially in taxa where developing young are directly exposed to the environment. Focusing on environmentally induced sex reversal offers a powerful approach for studying the genetic and developmental determinants of sex roles. Ample empirical evidence supports the role of cognition in mate choice, however, understanding the interplay of cognitive sex differences, sex roles, cognitive mate choice and its neuronal prerequisites needs further research. We encourage further work on diverse taxa to facilitate a comprehensive understanding of proximate and ultimate drivers of various sex roles manifesting in different breeding systems.

AUTHOR CONTRIBUTIONS

All authors contributed to writing and editing the article, approved the submitted version, and administered the Research Topic collection.

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