



## Introduction

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# Adult sex ratios and reproductive strategies: a critical re-examination of sex differences in human and animal societies

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It is increasingly recognized that the relative proportion of potential mates to competitors in a population impacts a range of sex-specific behaviours and in particular mating and reproduction. However, while the adult sex ratio (ASR) has long been recognized as an important link between demography and behaviour, this relationship remains understudied. Here, we introduce the first inter-disciplinary collection of research on the causes and consequences of variation in the ASR in human and animal societies. This important topic is relevant to a wide audience of both social and biological scientists due to the central role that the relative number of males to females in a population plays for the evolution of, and contemporary variation in, sex roles across groups, species and higher taxa. The articles in this theme issue cover research on ASR across a variety of taxa and topics. They offer critical re-evaluations of theoretical foundations within both evolutionary and non-evolutionary fields, and propose innovative methodological approaches, present new empirical examples of behavioural consequences of ASR variation and reveal that the ASR plays a major role in determining population viability, especially in small populations and species with labile sex determination. This introductory paper puts the contributions of the theme issue into a broader context, identifies general trends across the literature and formulates directions for future research.

This article is part of the themed issue 'Adult sex ratios and reproductive decisions: a critical re-examination of sex differences in human and animal societies'.

## 1. Introduction

The adult sex ratio (ASR), defined as the proportion of males in the adult population, has been implicated in both theoretical and empirical studies as an important driver of the evolution of mating systems, parental investment and reproductive competition [1–3]. Because the ASR varies not only at the level of species and higher taxa [4], but also within populations over space and time (e.g. [5–7]), it structures an individual's reproductive options and social interactions between those of the same and opposite sex. For example, variation in ASR has been shown to predict mating system and parental care across bird species [8], and both the formation and stability of pair-bonds across human populations [9–11]. However, because of the lack of inter-disciplinary exchange across the social and biological sciences, insights are slow to cross disciplinary boundaries and the role of the ASR in social and reproductive behaviour remains underappreciated and understudied. Through this theme issue, we aim to contribute to a conceptual, theoretical and methodological integration across disciplines to develop a more comprehensive understanding of the processes that link the ASR and behaviour. Achieving this goal is important not only for disciplinary advancement, but also for practical applications in many

fields—from human health and violence to population-level responses to climate change. Below we briefly introduce the theoretical underpinnings of research on reproductive strategies before presenting a conceptual overview of the contributions to this issue.

## 2. Theoretical foundations

While an individual's sex is a fundamental component of mating strategies [12,13], it is increasingly recognized that many sex-specific models of reproductive behaviour inadequately explain the highly variable patterning of mate acquisition, pair bonding and parenting both within and across species. Reproductive decision-making is a dynamic process, influenced by many individual, population- and context-specific characteristics [14–18]. Here, we focus on the ASR, whose important effects on mating behaviour in both human and animal societies have been recognized since early in the twentieth century, but largely remained unincorporated into active research programmes until about a decade ago. For example, sociologists Groves & Ogburn ([19], see also [20]) argued that the pattern of marriage in the USA followed principles of an economic market. They found that the proportion of marriageable members of the opposite sex influenced both rates of marriage and, perhaps more intriguingly, the relative importance of certain traits in a partner. Independent of this work in the social sciences, evolutionary biologist Mayr [21] highlighted the extreme variation in the ASR across various bird species, arguing that ASRs and mating systems were related. He noted that monogamy was generally more common under male-biased ASRs and polygyny under female-biased ASRs. Nonetheless, after decades of research, and despite partner availability being a fundamental demographic characteristic affecting mating options across populations, the role of the ASR in reproductive strategies remains poorly understood [2,3]. Given that partner availability has long been recognized to influence reproductive decision-making, why has the ASR not featured more prominently as an important predictor?

### (a) More males, more conflict

Darwin was the first to offer an evolutionary explanation for widespread sex role differences in his now famous distinction between male and female mating strategies, where he noted that males were often driven by a greater eagerness to mate than females [22]. This characterization of the 'ardent' male and 'coy' female quickly became rooted in the evolutionary sciences and was widely used to generalize reproductive behaviour across animal taxa, including humans. However, Darwin's ideas lacked a mechanism by which sex role differences were generated, even though he hypothesized '*that a numerical preponderance of males would be eminently favourable to the action of sexual selection*' (p. 146). Following from Darwin, Trivers [23] linked insight from Bateman's research [24] on sex differences in the fitness pay-offs from mating multiply with the differential parental investment in young by males and females. In its simplest form, Trivers' model posits that because males invest less initially, as a consequence of anisogamy, they have a higher potential reproductive rate [25] and benefit more from mating multiply than do females. As a consequence, it was argued that selection typically favours mate-seeking and competitive behaviour in males, and greater investment in parental care

by females. In an extension of this model, Emlen & Oring [15] incorporated variation in partner availability and predicted that as the number of available males relative to available females rises, so does antagonistic competition among males over the relatively fewer females. Under such intense sexual selection, males will be less likely to provide parental care after mating than females, creating positive feedback and selecting for greater investment in competition by males [1,2,26,27]. These expectations overlap with an influential literature in the social sciences. It is well documented that men are more violence-prone and competitive than women [28]. Accordingly, it is expected that as the number of men increases relative to women, rates of family and social instability will increase as well (due primarily to the growing number of unattached, bachelor males; [29,30]). Thus, there is a general expectation across literatures that a relative abundance of males will elevate levels of conflict (particularly between males over partners), reduce pairbond stability and decrease paternal investment.

### (b) More males, more investment

However, assumptions of sex differences in optimal mating rates and predictions of male-biased sex ratios elevating contest competition in males are increasingly being challenged. For example, several theoretical models that illuminate the possible origins for sex differences in parental care contend that anisogamy only sets the stage for, but does not determine, sex role evolution ([2,26], see also [31]). Furthermore, while this research highlights the importance of the ASR as a key predictor of sex role evolution, the relationship between partner availability and mating effort is in contrast with the effect as hypothesized by Emlen & Oring [15]. Specifically, a key feature of this framework is its game-theoretical approach [2,32], which incorporates the relative scarcity of partners when modelling the sex-structured pay-offs to reproductive behaviour [33,34]. While paternity certainty [35] and variability in mate quality [36] play key roles in sex role differences in reproductive effort, a central claim of this approach is that, in general, the profitability for males to invest in mating effort increases when more, not fewer, mating opportunities are available.

Males that pursue a mating-effort intensive strategy when mates are rare may find themselves spending longer periods of time between reproductive events than if they were to stay with their initial partner and care [2] or mate guard [33]. Thus, when males are in abundance and surrounded by competitors, they should reduce mating effort [37]. The ASR has since been shown to influence the coevolution of patterns of care and competition through varying sex-specific intensities of sexual selection both across and within species [8,14, 38–40]. These findings are in-line with mating market theory from the social sciences that also takes a frequency-dependent approach to behaviour [41,42]. The general expectation is that when males are rare they behave more promiscuously, offering little parental investment and are still able to obtain partners. However, when females are in short supply, males will be more willing to commit to a single partner and, depending on the culture under study, adopt behaviours consistent with female relationship preferences. Thus, according to these approaches, mating behaviour is seen as a response to sex-structured payoffs to partner availability.

### (c) Moving forward

Confusion regarding the effect of the ASR on behaviour is warranted given the current theoretical debate and lack of integration across the social and biological sciences (see, e.g. [43] for a cross-cultural review on violence). However plausible it may seem that male-biased sex ratios should be associated with rising levels of male mating effort and violent conflict, newer frequency-dependent models, as outlined above, are increasingly empirically supported. For example, in shorebirds with male-biased ASRs, male parental care (and even sex-role reversal) prevails, as in the case of jacanas (*Jacanidae*) and greater painted-snipes (*Rostratula benghalensis*); however, those species with female-biased ASRs, such as the ruff (*Philomachus pugnax*), have polygynous mating systems [8]. Similarly, in soapberry bugs (*Serinethinae*; [44]), males invest heavily in guarding their mates in response to partner shortages rather than continuing to invest in competitive efforts to acquire additional mates.

These results from frequency-dependent models are consistent with work on humans as well. For example, a study based in Columbia finds that family instability and male mating effort are elevated in response to an excess of women, not men. Specifically, marriage rates for men and women are lower and more men are involved in concurrent relationships in female-biased ASRs [11]. Cross-cultural research corroborates this pattern, revealing that female-biased sex ratios are associated with lower levels of male parental investment and higher rates of female-headed households [45]. Indeed, when there are too many men, the nature of relationships changes. For example, Angrist [46] found that among immigrants to the USA, strongly male-biased sex ratios had a large positive effect on the likelihood of female marriage and a large negative effect on female labour force participation. Additionally, Schacht & Borgerhoff Mulder [47] found that male investment in mating effort decreased with increasing partner rarity, with males focusing primarily on attracting a single partner at the most male-biased sex ratios. In general, male-biased human sex ratios are associated with a greater proportion of males married [9], less promiscuity in both sexes [45,48,49] and greater conjugal stability [50]. Thus, empirical support is growing for the general prediction that a male-biased sex ratio is associated with less male mating effort and antagonistic mating competition.

While current ASR research is proving fruitful, it has not been well integrated across disciplines, or across studies of humans and non-human animals. In an attempt to clarify the role of partner availability in behaviour, through this issue, we present research that offers theoretical, methodological and empirical advances in ASR research. We seek to facilitate and encourage inter-disciplinary integration across conceptual and methodological boundaries, highlighting the importance of understanding the multiple causes of ASR variation as well as the far-reaching consequences of this variation for sex-specific behaviour in non-humans and humans alike.

## 3. Road map to this theme issue

In this issue, we present 15 articles that contribute original research and reviews related to the causes and consequences of ASR variation, spanning the social and biological sciences.

In assembling this set of articles, we pursued three goals. First, we wanted to identify and begin filling gaps in our theoretical foundations underlying research on sex ratios. As briefly outlined above, recent research on the relationship between sex roles and the ASR challenges traditional approaches largely reliant on sex-based models of optimal reproductive strategies [2,27,32]. The first four contributions re-evaluate the theoretical foundations of sexual selection, sex roles and ASR research and address some fundamental methodological issues. Second, we aimed to catalyse integration across disciplines by demonstrating that the ASR has predictable effects on both animal and human behaviour related to sex roles. Importantly, results of empirical studies of ASR-related variation in competition and parenting in human and animal societies seem to converge, supporting recent reformulations in sexual selection and six articles in this issue broaden this comparative perspective with additional examples. Third, we wanted to emphasize the fact that variation in the ASR has consequences that go far beyond sex roles, including conservation biology and human health. Following on this, the final five contributions highlight some recent examples related to these topics.

### (a) Theoretical and methodological foundations

Clutton-Brock [51] provides a historical perspective on the development of key ideas in sexual selection theory and the role of the ASR on selection gradients. His key point is that, for a comprehensive understanding of mating systems, researchers should aim to estimate multiple measures of selection simultaneously because each reflects different evolutionary and ecological features. Moreover, reproductive competition, especially among females, is a neglected element of breeding systems, and he calls for studies that investigate selection on both males and females in a given population.

Jennions & Fromhage [52] review recent theoretical models and aim to clarify whether the ASR alone best predicts sex differences in competitive traits and parental care. They show that modelling behaviour over evolutionary versus ecological time can produce different outcomes, highlighting that predictions should match the time scale under study as well as the need for multi-generational datasets to empirically determine support for theoretical claims. Moreover, at least for the genetic evolution of traits, they argue that studies of reproductive behaviour need to pay attention to the effects of both the sex ratio at maturation and the risk of mortality related to caring and competing.

An accurate measure of the ASR is central to evaluation of ASR effects. Determining the number of adult males and females in a population seems straightforward, but is fraught with difficulties. Ancona *et al.* [53] summarize and discuss a number of practical problems associated with ASR estimates. Importantly, they note that previous studies have used various ways of expressing ASR, hampering comparisons across the literature. They propose the proportion of adult males ( $ASR = \text{number of adult males} / (\text{number of adult males} + \text{number of adult females})$ ) as the index with the most desirable mathematical properties and so contributors to this special issue apply this insight. Pollet *et al.*'s [54] contribution follows up on methodological issues related to the study of ASR, and focuses specifically on sampling issues related to research on humans. They caution that analyses of differing data

resolution could produce inconsistent results, further confusing comparisons of findings across studies.

### (b) Behavioural consequences

The next set of papers present new empirical results on the behavioural consequences of ASR variation on sex roles in a range of human populations and birds. Schacht & Smith [7] and Ugglå & Mace [55] make use of extensive, high-quality demographic data to explore multiple outcomes and heterogeneity of ASR effects across individuals. Specifically, Schacht & Smith [7] explore the consequences of a biased ASR for relationship and reproductive outcomes in a historical US population. They find that both the contributors to and consequences of ASR imbalance vary over time and, specifically, that indicators of male parental investment and female bargaining power are elevated in response to a surplus of men. Ugglå & Mace [55] also find that the ASR is associated with relationship outcomes. In this case, in contemporary Northern Ireland relationships vary across different types of individuals, and in particular men and women of lower socio-economic standing are more likely to provide paternal care and cohabit with a partner (respectively) in response to a male-biased ASR. The authors argue that the ASR is important to variation in the adoption of different strategies in response to partner availability different strategies in response to partner availability or scarcity. Loo *et al.* [56] build on previous mathematical models that explore the relationship between sex ratios and human male mating strategies. Through their modelling, they find that when the sex ratio is female-biased, multiple mating prevails, and when male-biased, mating guarding is more common, offering possible insight into the conditions under which monogamy evolved in humans.

Determining the causes of ASR variation remains an important task for comparative studies of sex ratios. Given various logistical challenges, datasets that provide a longitudinal perspective are particularly valuable. In their contributions, Kramer *et al.* [5] and Kappeler [6] explore the causes of ASR variation among hunter-gatherers and non-human primates, respectively. Among the Savannah Pumé hunter-gatherers, 25 years of demographic data show that random fluctuations in births and deaths generate significant year-to-year variation in the ASR. Migration at maturity is an important mechanism to manage local partner scarcity, and, as in other hunter-gatherers, dispersal patterns are non-sex-specific. Through theoretical modelling, they show that bi-sex dispersal manages stochastic ASR swings and offers a way to stabilize group composition. Kappeler's [6] overview of various non-human primate societies underpins the significance of group structure by arguing that the social unit is the most meaningful level for studying the behavioural consequences of ASR variation. Using examples from different primates, he also highlights the different temporal dynamics associated with the operational sex ratio [52] versus the ASR.

Of the behavioural consequences of ASR variation, sex differences in parental care have probably received the most theoretical and empirical attention. Exclusively maternal, exclusively paternal or biparental care are found in almost all classes of vertebrates [6], and the ASR has emerged as a robust predictor of the corresponding behavioural biases. In several species of fish, birds and mammals, parental care is also provided by non-breeding individuals. Does ASR also predict the occurrence of cooperative breeding and helper

sex ratio? Based on the results of a comparative study across nearly 200 species of birds, Komdeur *et al.* [57] report that cooperatively breeding species have significantly more male-biased ASRs than non-cooperative breeding species. Moreover, the ASR predicts the sex ratio of helpers. Because offspring sex ratios do not predict ASR in birds, sex-specific dispersal and other demographic mechanisms driving these patterns require further study.

### (c) Applications of adult sex ratio research

The final set of studies address several different issues that illustrate the broad implications of variation in the ASR for social behaviour as well as for population viability. China, which has fomented many of the contemporary concerns about the destabilizing influence of male-biased ASRs, was the focus of research by Zhou & Hesketh [58]. While a male-excess is commonly thought to result in greater social and family instability within a population, the authors temper and redirect this concern. They find that unmarried men, specifically those that are likely never to marry, are at greater risk for depression and suicide. Rather than directing their inability to acquire a partner outwards, these men appear to suffer mental health related health consequences.

Grosjean & Brooks [59] use data from the historically heavily male-biased penal colony of Australia to test whether past imbalances in sex ratios have persistent effects on contemporary relationship quality. They find evidence that present-day marital and life satisfaction are higher in areas that were more male-biased in the past. Pouget [60] explores sexual relationships, bargaining power and family outcomes in the contemporary USA. In many African-American communities, men are rare due to high rates of incarceration and mortality. Under these circumstances, female-biased sex ratios are associated with men having both more partners and concurrent partners, and women having greater variation in their number of male partners. Specifically, this study finds that when sex ratios are female-biased, greater mixing occurs between the core and periphery of social networks, leading to higher rates of HIV transmission.

Changes in ASR can impact a species' extinction risk via their effects on the mating system and ultimately population viability, especially in species with labile sex determination systems. Using a theoretical model and empirical examples, Wedekind [61] explores the consequences of disturbed environments for population sex ratios. He argues that environmentally driven feminization could be more common than currently thought, although the frequency of these phenotype-genotype mismatched individuals may significantly affect population dynamics. Bókony *et al.* [62] examine the effects of climate-driven sex changes on ASRs in ectotherms with either temperature-dependent sex determination or temperature-sensitive genetic sex determination systems. Globally rising temperatures and environmental contaminants threaten to distort population sex ratios, which, in turn, may disrupt evolved mating strategies and potentially lead to population decline or even extinction. The authors show with individual-based theoretical models that the type of sex determination (i.e. XX/XY or ZZ/ZW) can influence the trajectory of ASR changes across generations. These results clearly call for intensified monitoring of wild ectotherm populations to better assess changes in their ASR that might promote future population decline.

## 4. Discussion

Demographic profiles of many populations are changing around the globe. Central to this transformation is the increasing imbalance in the ratio of adult males to adult females. In humans, this has generated significant concern. Economic migrants, refugees and otherwise displaced people are introducing population-level change in many countries. Particularly alarming, both in the social science literature and in popular culture, is the movement of young, unmarried men and the possible impacts due to elevated levels of violence in response to a male-biased ASR [30]. Many animal species too are experiencing dramatic swings in ASRs. For example, climate change and pollution have been shown to alter the relative number of males to females in species with temperature-sensitive sex-determination and/or those that experience impediments to development in response to environmental contaminants [61,62]. Accordingly, studies of species conservation raise the concern that population-level viability is declining in response to uncertain environments. Thus, the possible negative consequences to human and animal populations of ASR imbalances are of real, and not just academic, concern.

In response to recent theoretical and empirical research, sexual selection theory is currently being reformulated [2]. Traditional approaches to reproductive decision-making in the social and biological sciences have focused on relatively rigid sex-determined roles and behaviour [23,24]. However, recent theoretical and empirical work has drawn attention to facultative reproductive strategies in response to partner availability. These insights have led to frequency-dependent rethinking of both the evolution and contemporary manifestations of sex roles across animal taxa [6]. Because the numbers of males and females in a population structure both individual reproductive options and interactions between those of the same and opposite-sex, the ASR is increasingly recognized a key demographic variable driving behavioural variability of both sexes.

While current sex ratio research is proving fruitful, ASR has not been well integrated across disciplines, or across studies of humans and non-human animals. This development may be due to the fact that theoretical, experimental and comparative analyses on the causes and effects of ASR variation are often carried out in isolation from each other, and that their time scales may also differ (e.g. exploring the evolution versus maintenance of a trait). In addition, researchers studying human versus non-human animals often use different terminology, methods and theory, making synergistic work challenging. However, results from parallel lines of inquiry often produce consistent results and could usefully inform one another. These findings challenge longstanding claims of greater male investment in mating effort and the pursuit of multiple partners in the face of mate scarcity. Furthermore, a new synthesis is highly timely given demographic shifts associated with ASR changes in globally significant economies (e.g. China, Germany), the emergence of important health issues that are related to reproductive decisions (e.g. HIV and other STIs) and species conservation in response to climate change.

The articles in this theme issue cover research on the ASR across a variety of taxa and topics. They offer critical re-evaluations of theoretical foundations within both evolutionary and non-evolutionary fields, and propose

innovative methodological approaches, present new empirical examples of behavioural consequences of ASR variation and reveal that the ASR plays a major role in determining population viability, especially in small populations [5] and species with labile sex determination systems [61,62]. Nonetheless, heterogeneity in findings exist both across the previous literature and within this collection of articles.

Importantly, a number of authors offer insight into both past and present variability in results within and across populations and species. First, several papers highlight the need for shared methodology across future studies and to focus, where possible, on the individual as the unit of analysis rather than outcomes at the population-level, which while being convenient is prone to inferential concerns (e.g., ecological fallacy). Second, differing ecological and cultural contexts may produce dissimilar responses to similar ASRs across populations. For example, in humans, sociocultural norms governing reproduction can alter the costs and benefits to a certain behaviour (e.g. social sanctions against divorce) and accordingly its frequency [7]. Third, individuals vary and this can lead to substantial variation in behaviour within a population. Partner availability may lead not only to sex differences in behaviour, but also individual variation due to social status, mate value and competitive ability. Accordingly, this collection of articles offers ways for researchers interested in ASR effects to focus and refine their predictions to a particular population under study.

Still, a number of open questions remain or have emerged from this theme issue. First, a vast majority of studies are correlational—either recording patterns within and/or between populations, or using phylogenetic analyses across extant taxa. The causative agent that induced these behavioural changes might not be the ASR, but rather a hidden variable not evaluated. We therefore encourage more experimental studies that directly manipulate ASR and measure the effects on sex roles. Second, studies of ASR, mating and parenting have been restricted to a modest sample of fishes, reptiles, birds and mammals including humans. There is a need to broaden the coverage of cultural groups and taxa to improve our understanding of the levels and magnitude of ASR variation and to allow more detailed studies of the relationship between ASR variation and life history traits. Third, most studies have used cross-sectional data and therefore, long-term evolutionary dynamics remain unexplored. Additional research on these and other topics will yield a more comprehensive understanding of the social and evolutionary processes affecting the behaviour of humans and non-human animals.

In conclusion, in spite of exciting recent results, the role of the ASR is not yet widely appreciated in studies of social behaviour. For this reason, here we present a series of contributions that critically evaluate recent developments in sexual selection theory, examine the role of ASR in behaviour and offer insight and policy recommendations related to species conservation, social justice and health. This theme issue includes work from scholars whose research is often separated by disciplinary boundaries, yet challenges traditional approaches to patterns of sex-differentiated behaviour. Such integration has not been attempted before across such a broad range of disciplines and animal taxa, and it is our hope that this theme issue will contribute to a comprehensive conceptual framework that will inspire and guide future research on this topic.

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