Sex roles and sex ratios in animals

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ABSTRACT

In species with separate sexes, females and males often differ in their morphology, physiology and behaviour. Such sex-specific traits are functionally linked to variation in reproductive competition, mate choice and parental care, which have all been linked to sex roles. At the 150th anniversary of Darwin's theory on sexual selection, the question of why patterns of sex roles vary within and across species remains a key topic in behavioural and evolutionary ecology. New theoretical, experimental and comparative evidence suggests that variation in the adult sex ratio (ASR) is a key driver of variation in sex roles. Here, we first define and discuss the historical emergence of the sex role concept, including recent criticisms and rebuttals. Second, we review the various sex ratios with a focus on ASR, and explore its theoretical links to sex roles. Third, we explore the causes, and especially the consequences, of biased ASRs, focusing on the results of correlational and experimental studies of the effect of ASR variation on mate choice, sexual conflict, parental care and mating systems, social behaviour, hormone physiology and fitness. We present evidence that animals in diverse societies are sensitive to variation in local ASR, even on short timescales, and propose explanations for conflicting results. We conclude with an overview of open questions in this field integrating demography, life history and behaviour.

Key words: sex roles, sex ratios, parental care, mate choice, sexual selection, demography, physiology.

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I. INTRODUCTION

Anisogamy – i.e. the fact that females produce fewer but larger gametes whereas males produce more and smaller gametes – generates numerous sex-specific adaptations in morphology, physiology and behaviour (Parker, Baker & Smith, 1972; Andersson, 1994; Schärer, Rowe & Arnqvist, 2012; Parker, 2014), which entail differences between females and males in the degree of mate competition, mate choice and parental care. Darwin (1871) noticed that females tend to be choosier than males about whom to mate with, and Bateman (1948) subsequently demonstrated that male reproductive success is more variable and increases more steeply with the number of mates than that of females ('Bateman gradient'). Sex roles have been defined as 'conventional', when females are choosier than males, and males are more likely than females to compete for mating opportunities. For species with a trade-off between mating effort and parenting, female-biased parental care has sometimes been added to this definition. When females and males exhibit opposite patterns, with females competing for mating opportunities and males being choosier (and providing more parental care), sex roles have been referred to as 'reversed' (e.g. Andersson, 1994; Safari & Goymann, 2021). Alternatively, Vincent *et al.* (1992) defined sex role reversal as '*that situation in which, contrary to the common pattern, females compete more intensely than males for access to mates*'. By focussing on a single trait, this latter definition offers a simple and pragmatic solution to the problem of how to classify ambiguous trait combinations. For example, it draws a useful line between species where male-only care is associated with female competitiveness (such as in jacanas or coucals) or not (such as in rheas, ostriches or many teleost fishes), depending on whether males face a trade-off between caring and seeking additional matings. While we think this definition of reversed sex roles works well, this does not imply that the same narrow focus on competitiveness should be applied to the term 'sex roles' in general – that is without the qualifiers 'conventional' or 'reversed'. Instead, herein we follow Kokko, Booksmythe & Jennions (2013) in using 'sex roles' as an umbrella term for any systematic sex differences in reproductive behaviour – including mate competition, mate choice and parental care. How and why components of sex roles vary have become key questions in evolutionary and behavioural biology (Kvarnemo & Simmons, 2013; Janicke *et al.*, 2016; Clutton-Brock, 2017), and we discuss their relationships with sex ratios in this review.

The Darwin–Bateman sex role paradigm (Dewsbury, 2005) has received substantial criticism (Ah-King, 2012), much of which has focused on the depiction of anisogamy as the key determinant of sex roles. It was noted that a sex difference in the variance in mating success, in particular, could arise exclusively from chance ('stochastic demography') and environmental factors that affected the encounter and re-mating rates of males and females (Sutherland, 1985; Gowaty, 2004). Criticisms also include value-laden connotations of the terms 'conventional' *versus* 'reversed' sex roles and their inconsistent application in different taxonomic lineages (Ah-King & Ahnesjö, 2013). The perception of sex roles also varies as a function of research experience and cultural background (Pollo & Kasumovic, 2022). Finally, close scrutiny and replication of Bateman's original experiments revealed methodological flaws that, together with selective presentation of key data (detailed by Hoquet, 2020), led some to reject the entire paradigm that built upon his original study (Gowaty, Kim & Anderson, 2012), and others to dismiss sexual selection theory altogether (Roughgarden, Oishi & Akcay, 2006).

These fundamental criticisms provoked a wave of conceptual, theoretical and empirical rebuttals (summarized by Morimoto, 2020). In particular, Kokko *et al.* (2013) addressed three major criticisms raised by Ah-King (2012). First, models invoking stochastic demography do not link the independent variables to sex differences in patterns of mate choice and mating competition, thereby failing to match well-established empirical patterns that show clear sex biases in mate choice, weaponry and parental care, albeit ones that vary across taxa. Second, the term 'reversed' sex roles is neither circular nor misleading when applied to interspecific variation. Third, and perhaps most importantly, the behavioural and demographic environmental variables proposed to be independent drivers of sex roles are themselves the result of sex-specific selection (see also Schärer *et al.*, 2012).

More refined metrics of sex differences in the intensity of sexual selection are now available, and these have also influenced the debate around sex roles (Anthes *et al.*, 2017). A recent meta-analysis demonstrated that the opportunity for sexual selection is generally higher, and the Bateman gradient generally steeper in males than females, indicating a

stronger fitness increase with mating success in males than females that can potentially be acted upon by selection (Janicke *et al.*, 2016). These estimates of the strength of sexual selection are also higher for males than females in species with female-biased parental care (see also Mokos *et al.*, 2021), but stronger sexual selection on males is not invariably linked to sex biases in parental care. Species with a more strongly male-biased opportunity for sexual selection also exhibit greater male-biased sexual size dimorphism, but this effect is weak, and the sex difference in the Bateman gradient does not predict interspecific variation in sexual size dimorphism (Janicke & Fromonteil, 2021). Importantly, sex roles can respond flexibly to variation in environmental factors that affect sex-specific selection (Janicke, David & Chapuis, 2015), with some species exhibiting stronger sexual selection in females (Janicke *et al.*, 2016). It is worth noting that variation in all dimensions of sex roles, including female competition and male choice, has been widely acknowledged and helped to keep sex roles in mainstream sexual selection research (Simmons & Gwynne, 1993; Parker & Simmons, 1996; Ahnesjö, Forsgren & Kvarnemo, 2008; Edward & Chapman, 2011; Stockley & Campbell, 2013; Parker, 2014; Hare & Simmons, 2019). In sum, sex roles are variable, even though the intensity of intrasexual selection is usually strongly male biased, as predicted by the Darwin–Bateman paradigm. Moreover, this strong sex bias cannot be explained by stochasticity, environmental variation or anisogamy alone.

Recent theoretical and empirical studies have identified the ratio of sexually mature individuals – the adult sex ratio (ASR) – as a key driver of sex roles (McNamara *et al.*, 2000; Kokko & Jennions, 2008; Székely, Weissing & Komdeur, 2014b; Fritzsche, Booksmythe & Arnqvist, 2016; Schacht *et al.*, in press), making the study of causes and consequences of variation in ASR highly relevant for the study of sex role evolution. This was already recognized by Darwin (1871, p. 146) who wrote that the relative proportion of adult individuals of one sex '*seem to fluctuate either during different seasons or in different localities in a sufficient degree to lead to (sexual) selection*' within species. But neither Darwin nor subsequent eminent evolutionary biologists such as Mayr (1939) had sufficiently detailed data or sophisticated theoretical concepts to link variation in ASR explicitly to sex roles. Today, theoretical, experimental and comparative evidence indicates that ASR is linked to processes of mate acquisition, breeding systems, patterns of parental care and sexual conflict, and influences individual fitness and the performance of populations. However, the role of ASR in generating variation in sex roles has not been systematically reviewed yet. Here, we first (Section II) provide an overview of how various measures of sex ratio relate to one another and review recent theoretical developments that highlight both the utility and limitations of ASR. Focusing on ASR, we then appraise patterns and causes of ASR variation within and among species (Section III). We then (Section IV) assess the consequences of ASR variation for sex roles, other aspects of behaviour,

physiology, fitness and conservation biology. Finally, we also mention potential feedback loops and provide a more comprehensive understanding of how sex roles and the ASR coevolve (Section IV).

II. SEX RATIOS

(1) Types of sex ratios

Sex ratios have played a key role in seminal studies in population biology, evolutionary biology and behavioural ecology (Fisher, 1930; Hamilton, 1967; Trivers & Willard, 1973; Charnov, 1982; Jennions *et al.*, 2017; Schacht *et al.*, in press). However, as the functional significance of a given ratio of males to females varies among demographic stages, the point in time when the ratio is calculated should be specified. Several milestones in age-structured populations are used to characterize sex ratios: the primary sex ratio (PSR) describes the proportion of males to females at fertilization; the secondary sex ratio (SSR) expresses the proportion of males to females at birth or hatching; the maturation sex ratio (MSR) refers to the proportion of males to females among individuals that reach sexual maturity; and the tertiary or ASR denotes the proportion of males to females among adult individuals (Fig. 1; Ancona *et al.*, 2017). The operational sex ratio (OSR), a widely used term in the context of sexual selection and breeding-system evolution, describes the subset of adult males and females that are currently ready to breed (Emlen & Oring, 1977; Kvarnemo & Ahnesjö, 1996).

While all sex ratios have been studied, some received greater attention than others because they are either conceptually more interesting when addressing evolutionary questions or they are less challenging to establish. The PSR has only been assessed in a few taxa (Khidr, Mayes & Hardy, 2013; Orzack *et al.*, 2015) because it often requires invasive handling. The SSR is easier to assess than the PSR and been of great interest because not all fertilized eggs develop until birth or hatching. The key insight attributed to Fisher (1930; but see Düsing, 1884; Edwards, 2000) is that, all else being equal, male and female offspring are predicted to be produced in equal numbers; a prime example of what has subsequently been defined as an evolutionarily stable strategy. The resultant sex allocation theory, which deals with deviations from baseline assumptions, has become a central topic in evolutionary ecology, and today there are countless studies examining how selection can lead to biased SSRs (West, 2009; Komdeur, 2012). The MSR has only recently emerged from theoretical models as a potential predictor of sex role divergence (Fromhage & Jennions, 2016, 2017; see Section II.3), but it is difficult to assess in species that are not strictly age structured. The OSR has long been recognized as an important predictor of sex-specific mating and parental strategies (Emlen, 1976; Weir, Grant & Hutchings, 2011; Kvarnemo & Simmons, 2013; Janicke & Morrow, 2018). However, it is highly dynamic because it changes in stable populations with every fertilization
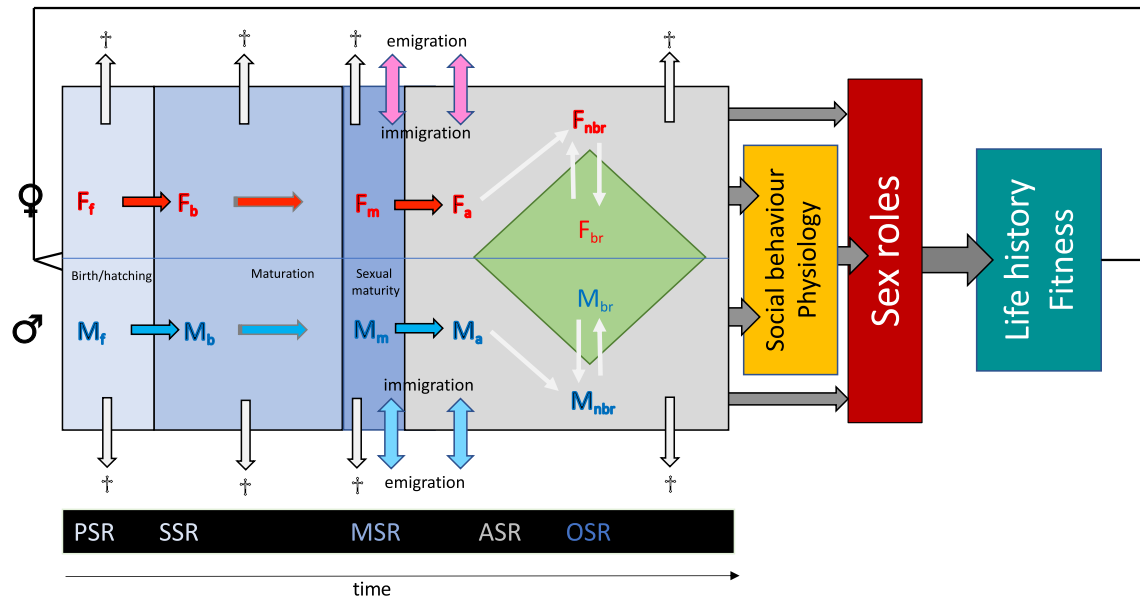
Fig. 1. The sex ratio can be specified at different points in time. It varies as a function of births of male and female offspring and sex-specific mortality, but also with immigration and emigration. Accordingly, different sex ratios can be determined based on the number of females (F) and males (M) at fertilization (f), birth (b), maturation (m), adulthood (a) and subsequently with breeding (br) or non-breeding (nbr) status. Different sex ratios are defined in Section II; † = death. Variation in ASR affects sex roles, presumably mediated by social behaviour and physiology, which, in turn, impact life-history traits, and, thus, ultimately fitness. PSR, primary sex ratio; SSR, secondary sex ratio; MSR, maturation sex ratio; ASR, adult sex ratio; OSR, operational sex ratio.

(Michener & McLean, 1996; Kappeler, 2017), and it is often challenging for researchers, but perhaps also for conspecifics, to identify an individual's breeding status. Finally, ASR can typically be determined with greater ease than MSR or OSR (Ancona *et al.*, 2017) and is often more suitable than the OSR when studying the relationship between sex ratios and sex roles, as outlined in Section II.2.

(2) ASR and OSR

The relationship between ASR and OSR is of particular interest because they both involve sexually mature individuals and because they have been used interchangeably in some studies. ASR and OSR are commonly, but incorrectly, assumed to be almost identical (Kokko & Jennions, 2008; Weir *et al.*, 2011; Neuhoff, 2017). Instead, the ASR refers to all adult individuals of a population, whether sexually active or not (Veran & Beissinger, 2009; Carmona-Isunza *et al.*, 2017), whereas the OSR is determined by the number of males and females that are available and actively seeking mates (Clutton-Brock & Parker, 1992). The OSR excludes sexually inactive and, in many cases, parenting adults (Székely *et al.*, 2014b) and reflects the availability of partners (i.e. mating opportunity; Székely, Webb & Cuthill, 2000). Therefore, ASR and OSR may substantially differ in wild populations and can exhibit rather distinct temporal dynamics (Carmona-Isunza *et al.*, 2017; Kahn *et al.*, 2021). This discrepancy is commonly due to the fact that the periods of sexual availability of males and females differ. The sexes

typically differ in the physiological constraints to prepare for breeding and in the duration of their fertile periods, leading to sex differences in potential reproductive rates (Clutton-Brock & Parker, 1992; Ahnesjö *et al.*, 2008; Kvarnemo & Simmons, 2013). In addition, females and males often contribute differentially to parental care, and their post-care recovery periods may also differ. Due to anisogamy, the sexes usually differ in their ability to remain in the mating pool. Sometimes males can still engage in matings even when providing parental care (Schwagmeyer, Mock & Bartlett, 2016; Araya-Ajoy, Dingemanse & Kempenaers, 2016; Safari, Goymann & Kokko, 2019), whereas females tend to be far more constrained from remaining in the mating pool while caring for offspring.

In addition, the time period during which an individual is sexually available for mating can vary due to phenotypic plasticity: animals may spend more time being sexually active when the chances of breeding are high, and the presence of many potential mating partners may entice some adults to reduce or even terminate parental care and seek a new mate (Székely *et al.*, 2000; Parra *et al.*, 2014). Therefore, the correlation between OSR and ASR can be rather weak (Carmona-Isunza *et al.*, 2017). Furthermore, ASR and OSR may covary when sex roles are fixed, but when they are flexible, a change in ASR can influence OSR, invoking a change in sex roles across the reproductive season (Amundsen, 2018). Most importantly, estimates of OSR, in our opinion, have important shortcomings in real life, because it is often hard to determine whether an individual

is sexually active or not. Sexual activity does not always produce clear visual, auditory or olfactory cues. And, as noted, many males are still able to fertilize females even if they are in a pair bond or caring for young (Schwagmeyer *et al.*, 2016; Araya-Ajoy *et al.*, 2016; Safari *et al.*, 2019), but their relative availability is unlikely to be the same as that of a mate-searching male. It is therefore often a matter of debate which individuals to include in the estimation of OSR.

ASR, by contrast, is a demographic property of populations that emerges *via* sex differences in mortality, maturation rates and/or movement (e.g. dispersal) patterns (Fig. 1; Le Galliard *et al.*, 2005; Regan *et al.*, 2020). It can, however, also vary without clear links to life history, phylogeny or environmental factors. For example, the ASR of 15 species of killifish (suborder Aplocheiloidei) hatched at equal sex ratios and maintained under identical laboratory conditions varied from 0.23 to 0.76, but neither phylogenetic closeness, annual or non-annual life-history strategy, nor keeping them alone or in groups had significant effects on ASR variation (Sowersby, Gonzalez-Voyer & Rogell, 2020). The OSR incorporates these factors but also emerges due to individuals' decisions about whether to join the breeding population, and how long to refrain from breeding during and/or after periods of parental care (Clutton-Brock & Parker, 1992; Kokko & Jennions, 2008). Because the OSR reflects short-term changes in mating decisions, parental care and post-care recovery, it is related to mate choice, pair bonds and parental care (Székely *et al.*, 2000; Jennions & Kokko, 2010). Therefore, the OSR can be viewed as both a cause and a consequence of the mating system, rather than an external causal factor (Székely *et al.*, 2000; Donald, 2007). This is also true of the ASR if sex differences in mortality, maturation and movement reflect reproductive decisions or strategies, such as fighting for territories or mates, delaying maturation to become more competitive, or moving to locations with less reproductive competition. However, given the ASR's dependence on demographic processes, the effect is likely to be weaker. We therefore suggest that ASR is generally a more useful measure, because it is easier to estimate in practice (Ancona *et al.*, 2017; Neuhoff, 2017), relies on fewer assumptions, and is more likely to be a cause rather than an effect of breeding system variation (Székely *et al.*, 2014*a*,*b*; Eberhart-Phillips *et al.*, 2018; Cox, Cusick & DuVal, 2019; Grant & Grant, 2019, but see Janicke & Morrow, 2018). Nonetheless, both measures may require information on the social system, and ASR may also vary on short timescales in some species, so that practical aspects of a given study system may influence their empirical measurement.

## (3) Theoretical foundations of the relevance of ASRs

Many species show sex differences in mating competition, mate choice and parental care. While all these behaviours potentially influence each other and tend to co-evolve, researchers have focused on the central role of parental care. Once one sex invests substantially more time and resources in offspring than the other sex, this has profound consequences for the economics of mate choice and mating competition because the OSR is usually biased towards the sex providing less care. The more-caring sex then pays a lower cost to be choosy about whom to mate with (Kokko & Johnstone, 2002), whereupon the less-caring sex gains more by competing for mates. The less-caring sex therefore has greater 'scope for competitive investment' (i.e. selection for traits that facilitate access to mates, even at a mortality cost; Kokko, Klug & Jennions, 2012). If one of the sexes incurs higher mortality – perhaps due to mating competition – then it becomes rarer and the ASR becomes more biased towards the caring sex.

Early models predicted that such an ASR bias would directly affect the evolution of sex-biased parental care (Yamamura & Tsuji, 1993; Houston & McNamara, 2002). For example, if males are the rarer sex, then their average reproductive rate must be correspondingly higher than that of females. This seems to imply that males gain more from returning to the mating pool quickly instead of providing care. This implication, however, rests on the problematic assumption that reproductive rates are a valid stand-in for lifetime reproductive success. If mortality differs between caring and competing, then care decisions affect both lifespan and reproductive rate; and both variables influence lifetime reproductive success (Jennions & Fromhage, 2017). This insight leads to a more nuanced picture in which only some sources of ASR bias – rather than the ASR itself – affect the evolution of parental care (Fig. 2). For example, if one sex is less likely to mature (=bias in the MSR) then it has higher reproductive value (=expected future reproductive success) and more to lose when it dies as an adult. If caring imposes a mortality risk, this asymmetry in reproductive value then affects the relative cost of caring. By contrast, if mortality during mating competition biases the ASR, then this does not affect the cost of caring (Fig. 2): the rarer sex's higher reproductive rate is perfectly compensated for by its lower survival (Fromhage & Jennions, 2016) and its reproductive value remains the same.

This caveat does not undermine the usefulness of the ASR for empirical research. From a philosophical perspective, it is unsurprising that the explanatory power of a summary statistic such as ASR must ultimately rest on lower-level causal mechanisms, the detailed analysis of which can bring out limitations of that power. How important such limitations are in practice is a separate matter, which has to be resolved empirically.

In addition, the ASR may affect sex roles in other ways, e.g. (*i*) through phenotypically plastic responses to local variation in OSR (Jennions & Fromhage, 2017); (*ii*) by changing the benefits of caring if adults of one sex are a greater threat to offspring (e.g. if only males are predators on young then a male-biased ASR increases the benefits of parental care, which will magnify the effect of any sex difference in the ability to protect offspring); and (*iii*) through qualitatively changing the mode of competition and selecting for different traits. A potential example here is the finding that – possibly mediated by a shift towards polygamy and high-stakes competition – the rarer sex in the ASR appears to have been selected for larger body sizes in amniotes (Liker *et al.*, 2021).
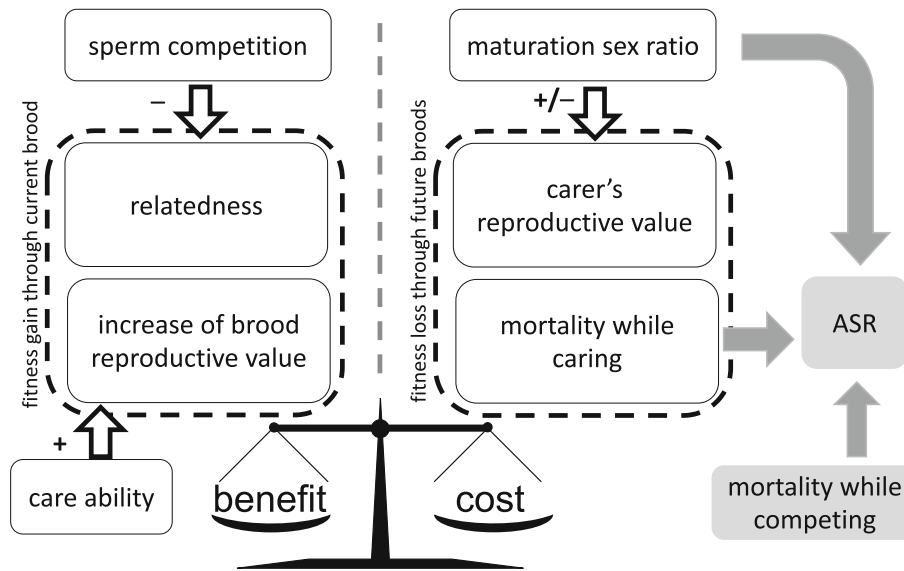
Fig. 2. Factors affecting the economy of parental care (simplified after Fromhage, 2017). A parent should provide care as long as the benefit (i.e. the marginal fitness gain through the current brood) gained outweighs the associated cost (i.e. the loss of potential future broods due to mortality while caring). Sex differences in the benefit may arise because of sperm competition, which from a male carer's perspective dilutes relatedness to the brood (indicated by −) and care ability, which increases the brood's survival and subsequent success (indicated by +). Sex differences in the cost may arise because the maturation sex ratio (MSR) is biased and the rarer sex, having higher expected reproductive success, has more to lose in the event of its death or because one sex incurs higher mortality while caring (e.g. due to sexual dimorphism). The adult sex ratio (ASR) does not directly enter this cost–benefit analysis, even though (other things being equal) it is correlated with both the MSR and the mortality while caring.

III. LEVELS AND CAUSES OF VARIATION IN ASR

(1) Levels of variation in ASR

Variation in ASR can be measured at multiple spatial scales, from the species level to that of the social unit (Fig. 3). In birds, where interspecific variation in ASR was first described (Mayr, 1939), the ASR was found to be balanced in only 35% of 183 species (Donald, 2007). Across a wider range of taxa, ASR was found to vary from a strong female bias in isopods (proportion of males 0.01) to a strong male bias in some birds (0.9; Székely *et al.*, 2014*a*). Broader trends across higher taxonomic levels also exist. For example, mammals frequently have a female-biased ASR, whereas ASRs in birds are more often male-biased (Donald, 2007), although even within a single genus strongly male- and female-biased ASRs may be found (e.g. *Charadrius* plovers; Eberhart-Phillips *et al.*, 2018).

Within species, ASR can vary markedly between the population level and the level of the social unit (e.g. species A and C in Fig. 3). In many group-living species, individual group sex ratios do not reflect that of the overall population. In extreme cases, such as in elephants (*Elephas* spp.), sperm whales (*Physeter macrocephalus*), and several temperate-zone bat species (e.g. *Myotis bechsteinii*), females form complex matrilineal societies, whereas males are either solitary or form all-male groups (Wittemyer, Douglas-Hamilton & Getz, 2005; Whitehead *et al.*, 2012; Kerth & van Schaik, 2012). Particularly at the group level, ASR can vary greatly among neighbouring groups (species B in Fig. 3).

For example, high ASR variation has been observed across groups of spotted hyenas (*Crocuta crocuta*; Vullioud *et al.*, 2019), Verreaux's sifaka (*Propithecus verreauxi*; Kappeler & Fichtel, 2012), and African striped mice (*Rhabdomys pumilio*; Schradin *et al.*, 2020). Finally, there can be substantial variation in ASR over time within a social group (see Section III.1). The significance of this variation depends, of course, on a given species' life history and generation time, but the key point is that the local ASR is not necessarily stable in a given habitat. It can vary over years, as seen in a marsupial population, where it changed more than twofold in just 5 years (Wayne *et al.*, 2015), or even within the course of a single breeding season [e.g. in wild populations of two-spotted gobies (*Gobiusculus flavescens*; Forsgren *et al.*, 2004) or turquoise killifish (*Nothobranchius furzeri*; Vrtílek *et al.*, 2018)].

When studying the causes of ASR variation, it is therefore important to define the unit of analysis. Specifically, the social organization of a given species, i.e. whether its members live a solitary life, in pairs, or in transient or stable groups, needs to be taken into consideration (Kappeler, 2019). Socially meaningful units of analysis, such as groups or populations, often exhibit variable ASRs across space and time, hampering the application of uniform criteria when choosing representative values for comparative studies. In addition, in birds and mammals there may be floaters living temporarily outside the main social units, who are easily missed in surveys, but who can have a strong impact on the reproductive strategies of residents (Zack & Stutchbury, 1992; Port, Kappeler & Johnstone, 2011; Huck *et al.*, 2014). Such logistic challenges can be overcome in
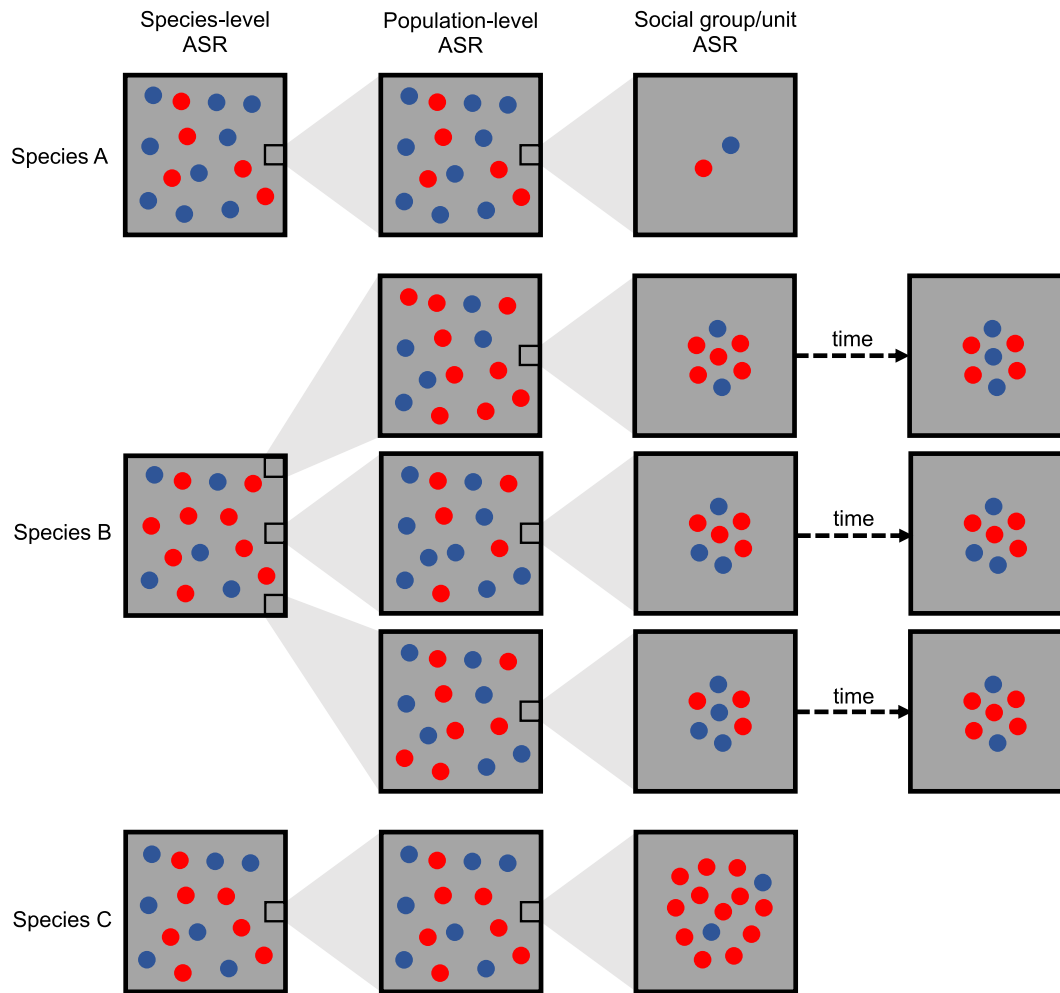
Fig. 3. Adult sex ratio (ASR) can vary among species, and at different spatial and temporal scales within species (blue circles represent males, red circles represent females). At the species level, populations may be male biased (species A), female biased (species B) or balanced (species C). Within species, the population-level ASR may approximate species-level ASR (species A and C) or vary among populations (species B). Individual social groups/units may vary strongly (species A and C) from the wider population (e.g. individual pairs, harem groups or female maternity colonies). Finally, ASR may vary over time, especially at the level of the social group (species B). The small squares with black outlines within the large squares representing species, populations and social units, indicate the enlarged portions of these levels of organization, e.g. the small square in the larger square representing Species A (top left) shows a population of that species.

long-term field studies of known individuals, which encompass detailed knowledge and data on the social organization and ecology (Clutton-Brock, Rose & Guiness, 1997; Kappeler, van Schaik & Watts, 2012).

An appreciation of intraspecific variation in ASR at different levels of social organization and temporal scales is not only important for conceptual reasons but also because it guides research on its causes and consequences. Depending on the study question, the biologically meaningful level of ASR variation for a group-living species may be the group, the wider neighbourhood, including other groups and potential floaters in the local population, or the long-term species-specific average. Empirical tests for variation in selection on the traits that define sex roles arising from biased sex ratios

should therefore distinguish between long-term evolution based on species-typical values, and adaptive flexibility based on plastic responses that constantly track the local ASR (Kokko *et al.*, 2012; Kappeler, 2017). It may be helpful for future comparative studies to emphasize this distinction by labelling these as the average and local ASR, respectively.

(2) Causes of variation in ASR

At all levels, ASR varies as a function of sex biases in fertilization, mortality, sexual maturation and dispersal (Veran & Beissinger, 2009; Kosztolányi *et al.*, 2011; Ancona *et al.*, 2020; Fig. 1). For example, biases in ASR can arise because of deviations from an even PSR at conception, biases

in SSR due to sex ratio distorters (e.g. *Wolbachia*), sex-biased mortality rates until sexual maturity, including mortality due to sex-biased natal dispersal (Kalmbach & Benito, 2007; Aleuy *et al.*, 2020), and sex differences in rates of sexual maturation or reproductive lifespan. This renders the study of causes of variation in ASR challenging, especially in long-lived taxa.

Locally (e.g. within groups), a bias in the ASR can be due to sex-specific reproductive strategies that influence the number of males or females per group. For example, at small female group sizes, single males are more likely to monopolize access to these females, resulting in the exclusion of other males and strongly female-biased ASRs of groups (Kappeler, 2013). Further, some adaptive behavioural responses to a biased ASR, such as increased mate harassment in male-biased populations (Le Galliard *et al.*, 2005), affect the ASR *via* sex-specific mortality rates. These types of responses can create interesting feedback loops, making studies of the causes of ASR variation particularly relevant to illuminate why the ASR and sex roles are correlated (Székely *et al.*, 2000, 2014*b*).

IV. CONSEQUENCES OF VARIATION IN ASRS

The reproductive strategies of males and females should be sensitive to the relative availability of potential competitors and mates, and, in taxa with non-obligate biparental care, decisions about parental investment should also respond to variation in ASR (albeit dependent on the source of ASR variation; see Section III). Because males and females differ in how they maximize their lifetime reproductive success, their reproductive strategies lead to sex differences in how they interact with members of their own and the opposite sex. As we show below (see Sections IV.1–4 and Table 1), empirical studies and experimental manipulations of ASR provide strong support for the predicted links between ASR and sex roles.

There are three main approaches to study the consequences of ASR variation for sex roles. First, interspecific comparisons can test for broad correlational patterns in the relationship between ASR variation and an aspect of sex roles (e.g. Eberhart-Phillips *et al.*, 2018; Liker, Freckleton & Székely, 2013, 2014; Liker *et al.*, 2021). Second, we can test

Table 1. Expected effects of adult sex ratio (ASR) variation (yellow = ♀ biased; blue = ♂ biased) on mate choice, sexual conflict, parental care, mating systems, social behaviour, hormone physiology and fitness, based on theory and the results of key studies summarized in Section IV. Study results are based on interspecific comparisons, long-term studies with spatial or temporal variation in the ASR, or experimental manipulations of the ASR. Note that phylogenetic and natural history of a taxon will have a strong influence on both the flexibility and direction of effects of a bias in the ASR, leading to seemingly contradictory observations in some cases.

		Predicted effects of ASR variation	
Mate choice	Choosiness	♀ Choosiness low	♂♂ And ♀♀ respond adaptively to changes in ASR that predict mating competition and mating opportunities
		♂ Choosiness low	
Sexual conflict	Intrasexual competition	♀–♀ Competition/aggression high	
		♂–♂ Competition/aggression high, or ♂ investment in parental care high	
	Mate guarding, courtship, reproductive tactics	♂ Investment in courtship low, ♀ resistance to mating low	
		♂ Mate guarding high, harassment and coercion of ♀♀ high, sneaky behaviours high, copulation duration high, ♀ resistance to mating high	
Parental care and mating system	Investment	♂ Investment and care low	
		♂ Investment and care high	
	Cooperation	♂–♀ Cooperation low	
		♀–♀ Cooperation low	
	Mating system	Polygyny	
		Polyandry	
Social behaviour	Affiliative intrasexual interactions	♀♀ And ♂♂ affiliative interactions may increase or decrease; little is still known about ASR effects on social behaviours (e.g. coalition formation, reconciliation, vigilance)	
Hormone physiology	Testosterone and glucocorticoids	♂ Testosterone high because ♂–♀ interactions frequent	
		♂ Testosterone high because of high ♂–♂ competition or low because of interference of testosterone with paternal behaviours ♀ Glucocorticoids high because of ♂ harassment	
Fitness	Reproductive success	Higher for the less-abundant sex than for the more abundant sex	

whether naturally occurring spatial or temporal intraspecific variation in the ASR predicts variation in the expression of sex-role-related traits over space or time if the sequence and context of events are known. Long-term, individual-based field studies are likely to offer particularly valuable insights into the effects of intraspecific temporal variation in the ASR (Kappeler, 2017; Regan *et al.*, 2020). The third approach is to conduct experiments and artificially manipulate the mean ASR to test predictions about the adaptive value of plastic or evolved responses to ASR variation. Such studies can test if experimental shifts in the ASR are causally related to changes in traits of interest in ways that increase an individual's fitness. Most empirical work has been conducted in the laboratory (Gao & Kang, 2006; Head, Lindholm & Brooks, 2008; de Jong *et al.*, 2009; Edward, Fricke & Chapman, 2010; Weir, 2013; Jehan *et al.*, 2020), under semi-natural conditions (e.g. outdoor pools; Mills & Reynolds, 2003), or in fenced natural areas (Le Galliard *et al.*, 2005; Rosa *et al.*, 2017; Heimerl *et al.*, 2022). Fewer experiments have been conducted in the field (Cox *et al.*, 2019). These studies have focused on a broad range of taxa, including fish (Mills & Reynolds, 2003; Head *et al.*, 2008; de Jong *et al.*, 2009; Wacker *et al.*, 2013; Weir, 2013; Liao *et al.*, 2014), birds (Cox *et al.*, 2019), lizards (Le Galliard *et al.*, 2005; Fitze & Le Galliard, 2008), snakes (Shine, Langkilde & Mason, 2003), insects (Gao & Kang, 2006; Edward *et al.*, 2010; Kelly, 2015; Fritzsche *et al.*, 2016; Godwin *et al.*, 2017; Rosa *et al.*, 2017; McNamara *et al.*, 2019; Jehan *et al.*, 2020) and spiders (Heimerl *et al.*, 2022).

ASR manipulation has been primarily used with the intention to increase the strength of sexual selection to test predictions about reproductive investment, trade-offs in life-history traits, parental care and sexual conflict. Studies applying manipulations during an individual's lifetime (within one or multiple breeding seasons) have demonstrated responses to changes in ASR across a broad range of traits. Male-biased ASR triggers increased male contest behaviour (common lizard, *Lacerta vivipara*; Le Galliard *et al.*, 2005), courtship (garter snake, *Thamnophis sirtalis parietalis* (Shine *et al.*, 2003); two-spotted goby (de Jong *et al.*, 2009)], nuptial gift production (nursery web spider, *Pisaura mirabilis*; Heimerl *et al.*, 2022), sperm investment (Chinese bushcricket, *Gampsocleis gratiosa*; Gao & Kang, 2006), post-mating guarding behaviour (New Zealand stick insect, *Micrarchus hystriculeus*; Kelly, 2015), parental care (i.e. nest attendance) (beetle *Lethrus apterus*; Rosa *et al.*, 2017), and changes in cooperative breeding behaviours (brown headed nuthatch, *Sitta pusilla*; Cox *et al.*, 2019). Female choosiness was shown to decrease in the butterfly *Bicyclus anynana* (Holveck, Gauthier & Nieberding, 2015), and senescence to accelerate in the mealworm beetle *Tenebrio molitor* (Jehan *et al.*, 2020) in male-biased ASR, whereas in the rosy bitterling (*Rhodeus ocellatus*) females actively increase courtship in female-biased ASR (Liao *et al.*, 2014).

Studies that have applied experimental evolution by rearing animals under a biased ASR for many generations are unsurprisingly focused on insects due to their short generation times and practicality for laboratory studies. Exposing fruit flies (*Drosophila* spp.) to experimental variation in ASR led to evolutionary divergence of several traits, including higher ejaculate depletion (Linklater *et al.*, 2007), increased testes size in males (Reuter *et al.*, 2008), higher female survival (Wigby & Chapman, 2004), changes in behavioural responses to rivals (Edward *et al.*, 2010) and in contest behaviour of both sexes (Bath *et al.*, 2021), in male-biased ASR. A reduction in immune function and loss of behavioural plasticity (Van Lieshout, McNamara & Simmons, 2014) was found in male-biased populations of seed beetles (*Callosobruchus maculatus*); female fitness decreased in female-biased populations (Michalczyk *et al.*, 2011) and sperm size increased in male-biased (Godwin *et al.*, 2017) populations of flour beetles (*Tribolium castaneum*); sperm production increased in male-biased populations (Ingleby, Lewis & Wedell, 2010) whereas immunity decreased (McNamara, Wedell & Simmons, 2013), and female genital morphology diverged in female-biased populations (McNamara *et al.*, 2019), but not the strength of male mate choice (Dougherty, Dewhurst & Lewis, 2020) in the Indian meal moth (*Plodia interpunctella*). Interestingly, females of the honey locust beetle *Megabruchidius dorsalis*, a sex-role-reversed insect with an evolutionary history of intense female-biased ASR, evolved to be more attractive under strong mate competition (Fritzsche *et al.*, 2016).

(1) ASR and mate choice

The strongest evidence for an effect of ASR variation on mate choice comes from experimental evolution studies. All else being equal, the rarer sex has more potential to choose mates but this potential is hardly ever realised because typically all else is not equal. For example, if the rarer sex in the ASR provides less parental care, then the OSR can be biased towards this sex, which increases the opportunity cost of rejecting a mate (i.e. being choosy) because there is a longer delay before encountering another potential mate (Berglund, Widemo & Rosenqvist, 2005).

Ah-King & Gowaty (2016) compiled studies that demonstrated a change in mate-choice behaviour caused by a long list of variables, including density, OSR and ASR. Out of 198 studies, only two manipulated the ASR and a few more the OSR (although OSR and ASR were often used synonymously). In Darwin's finches there was stronger size-assortative mating under a female-biased ASR, mediated by increased selectivity of females (Grant & Grant, 2019). And in a spider where males chose females there was more pronounced size-assortative mating with a male-biased ASR (Bel-Venner *et al.*, 2008). In the two-spotted goby, females preferred large males early in the season but no longer differentiated when males became scarcer (Borg, Forsgren & Amundsen, 2006). In three-spined sticklebacks (*Gasterosteus aculeatus*) males were less choosy when there was a male-biased ASR, but only if they were in poor condition (Candolin & Salesto, 2009). Similar effects have been shown

in arthropods. For example, female field crickets (*Gryllus pennsylvanicus*) became less choosy under a female-biased ASR (Souroukis & Murray, 1995).

The above examples demonstrate that animals seem to respond adaptively to changes in their social environment that predict mating competition or mating opportunities. Even though research is biased towards taxa that are more suitable for experimental research, it is likely that most animals have evolved the capacity to assess their mating opportunities and then adjust their choosiness by changing the likelihood that they reject potential mates. Even if changes in mate choice in direct response to the ASR have rarely been demonstrated, the ability to assess ASR changes serves as indirect evidence that the variation in ASR will influence mate choice. These responses have been shown to occur after exposure during the juvenile stage as well as during the adult stage. Indeed, responses to experimental manipulations of the ASR could be moderated by experiences as a juvenile, although this confounding factor has rarely been considered.

(2) ASR and sexual conflict over reproduction

The diverging evolutionary interests between individuals of the two sexes often result in conflict over mating, reproduction and parental care (Queller, 1997; Parker, 2006; Jennions & Fromhage, 2017), and both sexes have evolved adaptations and counter-adaptations to manipulate members of the other sex (Simmons, 2001; Arnqvist & Rowe, 2005). To gain paternity, males often adopt coercive tactics and females, in turn, have evolved behavioural, physiological and morphological traits and strategies to resist, evade or discourage male manipulation (Smuts & Smuts, 1993; Clutton-Brock & Parker, 1995; Gowaty, 2004; Bro-Jørgensen, 2011).

Variation in ASR can influence the type and extent of male coercive tactics (Darden *et al.*, 2009; Cureton, Martin & Deaton, 2010; Rossi, Nonacs & Pitts-Singer, 2010; Stumpf & Boesch, 2010; McNamara *et al.*, 2020) and even change male mating strategies. Under a male-biased ASR (and/or OSR) in species characterized by 'conventional' sex roles, males tend to be more aggressive and fight more often to outcompete rivals directly, at least when resources remain defendable and the costs of competing against many rivals are not too high (Weir *et al.*, 2011). For instance, male agonistic displays and interactions with other males increased with the number of competitors in mosquitofish (*Gambusia affinis*; Smith, 2007), sand gobies (*Pomatoschistus minutus*; Kvarnemo, Forsgren & Magnhagen, 1995), two-spotted gobies (Wacker *et al.*, 2013), field crickets (*Gryllus pennsylvanicus*; Cade & Souroukis, 1993) and European lobsters (*Homarus gammarus*; Debuse, Addison & Reynolds, 1999). Male–male aggression in male-biased ASRs can even result in lethal encounters, such as occur in spider monkeys (*Ateles geoffroyi*; Campbell, 2006). Similarly, female–female competition has been shown to increase with a more female-biased ASR [e.g. two-spotted gobies (Forsgren *et al.*, 2004)], Japanese medaka (*Oryzias latipes*; Grant & Foam, 2002). In

Chacma baboons (*Papio hamadryas ursinus*), years with a highly female-biased ASR were characterized by increased aggression among females (Cheney, Silk & Seyfarth, 2012). An experimental evolution study on fruit flies (*D. melanogaster*) showed that females – much more than males – evolved higher rates of same-sex aggression within 75 generations when the ASR was biased towards their own sex (Bath *et al.*, 2021).

There is little consensus on the effect of sex ratio variation on male courtship behaviour (de Jong *et al.*, 2012). At male-biased ASRs, mating opportunities for males are rare and, while increasing courtship effort may allow a male indirectly to outcompete rivals to gain access to females, due to lower mate availability it may instead pay to reduce costly courtship behaviours (reviewed by Bretman, Gage & Chapman, 2011; Weir *et al.*, 2011). Indeed, rates of courtship seem to decrease with the number of competitors and increase with the number of mates. This was shown for male guppies (*Poecilia reticulata*, Jirotkul, 1999), and for female and male Japanese medaka, which simultaneously compete and court mates (Clark & Grant, 2010). Similarly, in the two-spotted goby, a female-biased ASR may have led to the replacement of fierce male–male competition and intensive courtship behaviour in males with female–female competition and actively courting females (Forsgren *et al.*, 2004). Moreover, an extremely male-biased ASR may favour alternative reproductive tactics, such as sneaking behaviours, if increased investment in contest competition or costly courtship becomes uneconomical (Mills & Reynolds, 2003; Shine *et al.*, 2003; Weir, 2013). For example, male red-sided garter snakes (*Thamnophis sirtalis*) reduced their energetically demanding courtship when in large male-biased groups and switched to parasitizing the effort of other males (Shine *et al.*, 2003). In *Calopteryx* damselflies, males stopped being territorial and courting females when the number of males exceeded the number of available territories. Instead, males started to harass females to mate (Cordero & Andrés, 2002). Likewise, when the ASR became female-biased in agile frogs (*Rana dalmatina*), males switched from coercing females to mate to calling to attract females (Lodé *et al.*, 2004).

Male behaviours that enhance fertilizations in a competitive setting, such as mate guarding, are predicted to intensify with an increase in male bias in the ASR (Harts & Kokko, 2013). For example, male stick insects (*Micrarchus hystriculeus*) increased post-mating guarding intensity at male-biased ASR (Kelly, 2015). Similarly, males of the snapping shrimp (*Alpheus angulatus*) spent less time guarding recently mated females when the sex ratio was female-biased (Mathews, 2002). Prolonged copulation duration similarly functions as a form of mate – or ejaculate – guarding that can vary with the ASR. For example, copulation duration doubles with a shift from a female-biased to male-biased sex ratio in firebugs (*Pyrrhocoris apterus*; Schöfl & Taborsky, 2002). In polyandrous species, competition for fertilizations is known to affect ejaculates: males produce larger ejaculates when there is an increased risk of sperm competition until the intensity of competition is such that the rate

of return per sperm declines, favouring smaller ejaculates (Parker, Simmons & Kirk, 1990; delBarco-Trillo, 2011; Kelly & Jennions, 2011). Sperm investment (Linklater *et al.*, 2007) and sperm-allocation patterns (Ingleby *et al.*, 2010) diverged in response to an evolutionary history of biased ASR in *D.melanogaster* and the Indian meal moth. Qualitative ejaculate traits are also affected by increased exposure to other males or a change in the sex ratio (Magris, 2021), with male-biased conditions appearing to drive changes in ejaculate protein composition in *Drosophila* (Hopkins *et al.*, 2019). Females also compete and can use chemical weapons to influence each other's fertility. For example, in female-biased populations of the red flour beetle (*Tenebrio castaneum*), females upregulated the production of chemical weapons (quinones) that suppressed their rivals' reproduction, whereas in male-biased populations they downregulated production of quinones, which increased mean female fecundity (Khan *et al.*, 2018).

Allowing a population to evolve under a biased ASR for multiple generations has also been shown to drive evolutionary changes in morphological traits, such as increased testes size in female-biased populations, presumably due to a high male mating rate elevating the need for sperm (e.g. *D. melanogaster*; Reuter *et al.*, 2008), or longer sperm at male-biased ASR due to greater sperm competition (e.g. *T. castaneum*; Godwin *et al.*, 2017).

The ASR can alinfluence how females resist male coercion. For example, at a female-biased ASR female Indian meal moths evolved less-effective genital teeth to counter male genital coercion (McNamara *et al.*, 2019). In feral chicken (*Gallus gallus domesticus*), females plastically responded to a male-biased ASR by increasing their resistance to mating and by shifting their daily mating pattern to the evening to reduce harassment by males (Løvlie & Pizzari, 2007). *Gerris odontogaster is* a waterstrider species where females elude copulation attempts of males by repeatedly performing backward somersaults. As the density of males increased, females became less reluctant to mate (Arnqvist, 1992*a*,*b*,*c*). Generally speaking, in species where males cannot completely monopolize females, the ASR influences the level of control each sex can exert over the other *via* its effect on the local mating market; the fewer females are available to mate per male, the more 'bargaining power' females have over males (Noë, 2017; Kappeler, 2017). The coevolution of behavioural and morphological traits in females and males due to sexual conflict often takes unexpected routes. For instance, in the seed beetle (*Callosobruchus maculatus*), males harm females during copulation and females kick males to shorten copulation duration. When sexual conflict was experimentally elevated by increasing the male bias in the ASR, males evolved to be more harmful whereas female resistance remained unchanged (McNamara *et al.*, 2020). This might represent an evolutionary lag in female responses to male adaptations, and the sex currently 'winning' the evolutionary contest may change through time (Kokko & Jennions, 2014). The extent to which feedback loops changing the ASR affect the long-term trajectory of sexual conflict remains unclear.

(3) ASR, parental care and mating systems

The degree of parental care, defined as '*any form of parental behaviour that appears likely to increase the fitness of a parent's offspring*' (Clutton-Brock, 1991, p. 8), varies widely both within and among species. It ranges from no care, uniparental female or male care to biparental care (Webb *et al.*, 1999). In many taxa, females are more likely than males to care for offspring (Jennions & Fromhage, 2017). Theoretical, experimental and comparative studies have identified important links between the nature and degree of parental care expressed by each sex and biases in the ASR (Kappeler, 2017). According to theory, the probability that an individual will exploit the parental investment of its mate and reduce its own investment increases as the cost of finding a new mate decreases (Lessells, 1999). The relative gains from pursuing additional breeding partners (or fertilization opportunities) *versus* investing into parental care will usually differ between females and males because of differences in the availability of additional mates, which is partly related to the ASR (Trivers, 1972; Kokko & Jennions, 2008; Lessells, 2012) and what the OSR intends to measure. The sex that benefits more from seeking additional fertilizations (e.g. because mates are readily encountered) or that loses less from reducing parental care (e.g. because it has a lower confidence in genetic relatedness to the offspring that is cared for) should therefore respond plastically and seek out additional mating partners and decrease or abandon care. If, however, additional mating partners are rare, then the best strategy for both sexes may be to stay and care for offspring (Emlen & Oring, 1977; Owens & Bennett, 1997; Kokko & Jennions, 2008; Kvarnemo, 2018).

There is evidence that individuals respond adaptively to local variation in mate availability, often associated with changes in the ASR. For example, in fairy martins (*Petrochelidon ariel*), males reduced participation in incubation when the availability of fertile females increased (Magrath & Elgar, 1997). In Chinese penduline tits (*Remiz consobrinus*), males deserted early in the season, when they were still likely to find additional mating partners, but provided care later in the season, when the availability of mates declined (Zheng *et al.*, 2021). In two species of Darwin's finches, females were more frequently polyandrous in populations with male-biased ASR (Grant & Grant, 2019), and in agile frogs ASR variation seemed to drive the evolution of polyandry by modifying intrasexual competition (Lodé, Holveck & Lesbarreres, 2005). In cichlids, an experimentally induced surplus of females resulted in male desertion and reduced pair-bond stability (Keenleyside, 1983). In addition, some studies have experimentally imposed variation in the mating system, enforcing evolution *via* monogamy *versus* polyandry (e.g. Edward *et al.*, 2010). Although not addressed in depth here, these studies have a strong heuristic value because they induce biases in the ASR. In mammals, where females provide most post-zygotic care due to the biological constraints of internal gestation and lactation, and where exclusive paternal care does not occur, males may still increase offspring fitness in several ways that might be linked to the ASR but remain untested (Clutton-Brock, 2017; West & Capellini, 2016). For instance,

one could test if intraspecific variation in indirect forms of paternal care, such as protection from major hazards, is linked to ASR variation in primates or other mammals (Kappeler, 2017). There is also evidence that consistent differences in the ASR across species or populations are correlated with sex-specific patterns of parental care. For example, in shorebird populations with biased ASRs, offspring are predominantly tended by a single parent (Eberhart-Phillips *et al.*, 2018), suggesting that biased ASRs reduce parental cooperation and increase rates of divorce and infidelity (Liker *et al.*, 2013, 2014). In coucals, male-biased ASRs are associated with female competition and male-only care (Goymann *et al.*, 2015; Safari & Goymann, 2021).

In combination, these studies suggest that ASR variation affects sexual conflict over parental investment when the ASR varies due to external factors such as environmental perturbations (e.g. in Darwin's finches) or sex-biased predation (e.g. in agile frogs). In cases where biases in the ASR are intrinsic rather than caused by (stochastic) environmental perturbations, disentangling cause and effect is more difficult. For instance, in black coucals (*Centropous grillii*) it is unclear whether sexual selection led to an initial male bias in ASR (thereby reinforcing sexual selection on males and sexual conflict over mating and parenting) or whether an initial male bias in the ASR drove sexual selection (thereby reinforcing the ASR bias and sexual conflict). However, once slight sex biases in ASR or sexual selection have been established, strong positive feedback loops can begin to take effect and further enhance initial biases in sexual selection or the ASR (Andersson, 2004, 2005).

Theoretical models on how the ASR shapes sex roles in mate competition and parental care usually do not consider the phylogenetic history of taxa, thereby assuming that sex roles of both sexes have all degrees of freedom to evolve. This allows for greater generality of predictions, but it neglects the fact that the evolutionary thresholds for sex role evolution may differ among taxa (Andersson, 1995, 2005; Klug, Bonsall & Alonzo, 2013; Ligon, 1999). For instance, the prolonged period of embryo development inside the body of female mammals and the need for the young to be fed on milk from the mammary glands predispose female mammals towards exclusive nutritional care (Ligon, 1993). This may explain why direct paternal care is so rare in mammals as compared for instance to birds. Millenia of physiological trait evolution make it almost impossible for male mammals to respond to a male-biased ASR with investment into paternal care. Instead, they are constrained to increasing competition. Hence, it is not surprising that a strongly male-biased sex ratio in North Atlantic right whales (*Eubalaena glacialis*) promotes extreme male competition rather than male-only care (Frasier *et al.*, 2007), supporting the original idea of Darwin (1871) and Trivers (1972) that members of the more common sex should compete more strongly for access to the limited sex. By contrast, in bird species in which males are physiologically capable of incubation (e.g. shorebirds, woodpeckers, coucals), a male-biased ASR can result in male-biased offspring care (Eberhart-Phillips *et al.*, 2017; Liker *et al.*, 2013;

Székely *et al.*, 2014b), thus supporting recent theory according to which the more common sex should invest into parental care rather than competing for mates (Fromhage & Jennions, 2016; Jennions & Fromhage, 2017; Kokko & Jennions, 2008). Males of some other bird species (for instance, many passerines, hummingbirds, ducks and galliforms) lack the necessary morphological and physiological prerequisites to incubate eggs (a vascularized brood patch). Thus, unless males of such species 'reinvent' incubation first, they are constrained to responding to a male-biased ASR with higher competition. Hence, a uniform response of all taxa to biases in the ASR is not expected. Each taxon faces different phylogenetic (physiological) constraints that limit its options to respond to biases in the ASR.

(4) ASR and social behaviour

Relatively little is still known about how ASR shapes intraspecific variation in non-reproductive social interactions such as agonism or affiliation with members of the same and opposite sex (Kappeler, 2017; Clutton-Brock & Huchard, 2013; Davidian *et al.*, 2022). Variation in same-sex relationships because of changes in ASR has, however, been documented in species ranging from insects to birds and primates. For example, in an experimental evolution study, male fruitflies (*D. melanogaster*) fought more often at food patches in male-biased populations than in female-biased populations, although overall aggression rates did not differ between the two populations (Bath *et al.*, 2021). By contrast, in female-biased populations, where female competition for resources is higher, rates of aggression among mated females increased, including levels of postmating aggression (Bath *et al.*, 2021). In a feral horse (*Equus caballus*) population, a male-biased ASR led to a reduction in harem size, increasing the total number of social groups. As there was little evidence that females changed bands more often at male-biased ASRs, this change in social organization likely resulted from bachelor males forming new bands with dispersing subadult females. Subadult females were also less likely to breed, possibly because they were harassed by bachelor males (Regan *et al.*, 2020). In blue tits (*Parus caeruleus*), female-biased immigration caused severe competition among females, resulting in more polygyny, which was costly for females as they received less paternal assistance from males (Kempenaers, 1994).

Across 14 species of primates, a more male-biased ASR was linked to reduced reciprocity of female grooming, suggesting that female competition for males affects female grooming relationships (Hemelrijk & Luteijn, 1998). In addition, male-biased ASRs can elevate the general level of male–male aggression, resulting in lethal encounters in spider monkeys (Campbell, 2006).

Variation in ASR has been shown to affect non-reproductive male–female interactions. For example, in male-biased populations of the common lizard, males directed more aggression towards females, whose survival and fecundity dropped, causing a long-term population decline (Le Galliard *et al.*, 2005). Similarly, male-biased sex ratios

increased male aggression towards females, including even lethal injuries, in Hawaiian monk seals (*Monachus schauinslandi*), which further increased the male bias in their ASR (Johanos *et al.*, 2010). An intervention to remove males that brought the ASR back to parity reduced female mortality. In mountain gorillas (*Gorilla berengii*), male–female relationships were weaker, as measured by spending less time in closer proximity, in groups with more males (Rosenbaum, Maldonado-Chaparro & Stoinski, 2016). In olive baboons (*Papio anubis*), a female-biased ASR caused by the sudden death of half the males from tuberculosis led to a more relaxed dominance hierarchy and an increase in male–female affiliation (Sapolsky & Share, 2004). Finally, a study of 22 primate species from all major taxonomic groups showed that female dominance over males increased with the average proportion of males in a group (Hemelrijk, Wantia & Isler, 2008). In sum, variation in ASR affects both within- and between-sex relationships through changes in rates of aggression or affiliation, but how other behaviours (e.g. coalition formation, reconciliation, and vigilance) change remains understudied (Kappeler, 2017).

(5) ASR and hormone physiology

Sex-specific reproductive strategies are often underpinned by physiological differences. Hormones play a key role in shaping competition with rivals of the same sex, interactions with mating partners, and parental behaviour; and hormone levels are themselves affected during such interactions. Behavioural shifts associated with biased ASRs are therefore likely to be accompanied by changes in hormone concentrations. For instance, testosterone increases the persistence of aggression in male vertebrates (Wingfield *et al.*, 2006), and its concentrations are modulated by competition and mating activities (Wingfield *et al.*, 1990; Zimmermann *et al.*, 2017; Goymann, Moore & Oliveira, 2019). In male birds, peak testosterone levels are related to success in siring extra-pair offspring (Garamszegi *et al.*, 2005), and testosterone levels in the upper physiological range suppress paternal care (Goymann & Flores Dávila, 2017). Competition among males in species where females mate with multiple partners is also influenced by numerous physiological adaptations that promote success in sperm competition (Wigby *et al.*, 2020) or lead to female reproductive competition.

To date, no experimental studies of animals that have manipulated ASR have tested whether this affects steroid hormone levels. Some of the best evidence for a link instead comes from studies on humans. For example, changes in salivary testosterone of participants in a frisbee tournament depended on the ratio of women to men watching the game. Both female and male competitors showed a larger rise in testosterone when the sex ratio of the audience was biased towards the opposite sex (Miller, Maner & McNulty, 2012). There are also indirect lines of evidence that the ASR affects steroid hormone levels in animals. For example, in quail (*Coturnix japonica*), the testosterone response of two fighting males depended on whether or not females were watching (Hirschenhauser, Gahr & Goymann, 2013); and in a

population of western gulls (*Larus occidentalis*) with a female-biased ASR (which is unusual for a bird), the magnitude of the difference in testosterone levels between females and males was lower than expected based on values in other bird species (Wingfield *et al.*, 1982). It was, however, unclear if males had low testosterone levels due to reduced competition for females or if females had unusually high levels of testosterone due to increased competition among females.

In mammals and birds, experimental studies have shown that the presence of a reproductively active female typically elevates testosterone levels in males (e.g. Dufty & Wingfield, 1986; Goymann, East & Hofer, 2003; Pinxten, de Ridder & Eens, 2003). By contrast, simulated challenges among males with playbacks and decoy presentations rarely lead to an increase in testosterone for most vertebrates [reviewed by Goymann *et al.* (2019) and Moore, Hernandez & Goymann (2020)]. If a biased ASR changes sex steroid concentrations, then it is reasonable to assume that interactions between the sexes are likely to be more effective than those among members of the same sex. If the ASR is female biased, one might predict that testosterone levels of males will rise because of more frequent interactions with females. At male-biased ASRs, the story may, however, be more complicated: the Challenge Hypothesis predicts rising testosterone concentrations due to greater competition among males (Wingfield *et al.*, 1990) but this may not be reflected in the testosterone profile of males due to confounding effects (Goymann *et al.*, 2019; Moore *et al.*, 2020). For example, when a male-biased ASR increases male parental care, testosterone levels of males might even show a net decrease because high levels could interfere with paternal behaviours (Goymann *et al.*, 2019).

Interactions with conspecifics also affect female physiology. In vertebrates, one way that male courtship behaviour affects female physiology is by changing the secretion of gonadotropins and oestradiol (Bentley *et al.*, 2000; Cheng, 2003, 2008; Watts, Edley & Hahn, 2016; Lynch, Azieva & Pellicano, 2018). It is therefore possible that a shift in ASR that changes male courtship behaviour will affect the sex steroid profile of females. Agonistic interactions among females, which become more frequent when the ASR is female biased, may also affect their hormone concentrations. For instance, progesterone concentrations decreased during simulated territorial intrusions in female black coucals and progesterone implants decreased territorial aggression (Goymann *et al.*, 2008). Finally, when a male-biased ASR leads to more scramble competition and greater male harassment of females, this may affect female physiology: female red-spotted newts (*Notophthalmus viridescens*) had higher corticosterone and testosterone concentrations when the sex ratio was male-biased than when it was female-biased (Aspbury *et al.*, 2017). More studies that experimentally manipulate the ASR and measure the physiological consequences are urgently needed.

(6) ASR and fitness

Theoretical models show that the ASR can influence both female and male fitness and reproductive skew by changing

the competitive regime, the opportunities for mate choice and the scope for competitive investment into traits that increase access to mates (Kokko *et al.*, 2012; Courtiol *et al.*, 2016). If the ASR influences sex-role-related traits and behaviours, it should play a role in driving sexual selection on traits that affect access to mates, pair bonding and, by extension, parenting. For example, the evolution of sex-biased parental care is related to the ratio of males and females 'qualified to mate' as this determines the rate of return when deserting offspring return to the mating pool (Queller, 1997; McNamara *et al.*, 2000; Kokko *et al.*, 2012); and the ASR is an integral component of this ratio.

Theoretical and empirical studies have shown that changes in the competitive regime and mate-choice patterns of females and males can strongly influence their fitness (Kokko *et al.*, 2003; Alonzo, 2010; Clutton-Brock & Huchard, 2013). For instance, in several bird species, ASR was found to influence fledging success (Pilastro *et al.*, 2001; Dhondt & Adriaensen, 1994). This suggests that ASR can play a key role in driving sexual selection on traits related to access to mates, pair bonding and parenting which can impact Darwinian fitness.

Several empirical studies testing this hypothesis found that a relatively male-biased ASR was indeed associated with low male fitness and a less male-biased ASR with high male fitness or low female fitness. For example, in the agile frog, froglet survival and average number of clutches per male was diminished in populations with a more male-biased ASR (Lodé, 2009). In Hermann's tortoises (*Testudo hermanni*) a scarcity of females induced homosexual behaviours in males, which negatively affected male fitness (Bonnet *et al.*, 2016). In the blue-banded goby (*Lythrypnus dalli*), male mating probability and reproductive success was higher on reefs with relatively female-biased ASR than on reefs with more male-biased ASR (Kappus & Fong, 2014). Similarly, in the strawberry dart-poison frog (*Dendrobates pumilio*), the level of polygyny and male mating and reproductive success were higher when the ASR was female-biased (Prohl, 2002). In the mosquitofish, female reproductive success was reduced at relatively female-biased ASR despite low levels of male harassment (Smith, 2007). Finally, male-biased sex ratios can also impact the reproductive success of the sexes differently. In white-faced capuchin monkeys (*Cebus capucinus*), males had lower reproductive success in groups with more males, whereas female reproductive success increased, supporting the notion that the sexes have a conflict of interest over a group's ASR (Fedigan & Jack, 2011).

Long-term experimental evolution studies on insects showed that non-sexual interactions and mechanisms can also drive ASR effects on fitness. In the flour beetle, male-biased ASR increases female fitness relative to that in unbiased or female-biased groups (Michalczyk *et al.*, 2011): females use toxins as weapons for female-specific, density-dependent interference competition that suppresses female reproduction (Khan *et al.*, 2018). And in *D. melanogaster*, males evolving under male-biased ASR sired fewer offspring than control males, most likely as a result of faster rates of ejaculate depletion (Linklater *et al.*, 2007).

Theoretical studies suggest that ASR variation can affect not only individual fitness but also population fitness (i.e. average absolute fitness), and thus population dynamics (Rankin & Kokko, 2007). This notion is supported by empirical studies in fish and birds (e.g. Maan & Taborski, 2008; Heinsohn *et al.*, 2019) as well as a meta-analysis of experimental evolution studies that manipulated the presence or strength of sexual selection (usually by altering the ASR), and suggested that sexual selection can alter overall population fitness (Cally, Stuart-Fox & Holman, 2019).

(7) ASR and conservation

While a bias in ASR will usually alter the effective population size, its conservation implications have been largely neglected. Yet, population viability analyses demonstrated that a predator-induced strongly male-biased ASR in the swift parrot (*Lathamus discolor*) not only changed the mating system and impacted individual fitness but also contributed to the severe decline of this critically endangered species (Heinsohn *et al.*, 2019). Similarly, temporal changes in demographic attributes occurred in a critically endangered population of a small marsupial (*Bettongia penicillata*), including an important increase in the bias in the ASR a few years into the population decline (Wayne *et al.*, 2015). An excess of males in common lizards resulted in more sexual aggression against females, whose survival and fecundity then dropped (Le Galliard *et al.*, 2005). Ultimately this amplified the male bias and the total population size declined dramatically, as revealed by numerical population dynamics projections over many generations. Finally, in species with environmental sex determination, climate change-related effects can lead to extreme biases in hatchling sex ratios that distort ASR and that jeopardize population demography and genetics (Wedekind, 2017). In conservation biology, a biased ASR can potentially be used as an indicator of fragmented populations. For instance, in most birds females disperse whereas males are philopatric. A male-biased ASR could therefore indicate a fragmented or island population because female immigrants are rare due to the distance between neighbouring populations (Dale, 2002). The potential implications of the ASR for population biology should therefore be more broadly studied by conservation biologists.

V. CONCLUSIONS

(1) In this review, we have highlighted the links between sex ratios and sex roles. Despite some recent criticism, sex roles exist. They offer a useful concept to analyse sources of variation in mate choice, mating competition and parental care. Sex differences in associated morphological and other behavioural traits are empirically well supported, and were already identified by Charles Darwin over 150 years ago.
(2) Of the proposed evolutionary drivers of variation in sex roles, we suggest that the ratio of adult males to females in a population (ASR) offers a broader explanation than

anisogamy or environmental stochasticity. In addition, the ASR has the advantage that it is usually easier to quantify than the proportion of males and females ready to mate at any given point in time (i.e. the operational sex ratio, OSR), which has frequently been invoked in previous studies. (3) We highlight that the ASR is highly dynamic, and varies widely in space and time, that the meaningful level of analysis (group, population, species) varies depending on the question being asked, and that the link between the ASR and OSR is not straightforward.

(4) Our review demonstrates that variation in the ASR affecting sex roles is not only supported by correlational studies, but also by a growing number of experimental studies that have manipulated the ASR. Behavioural and physiological components of sex roles respond to variation in ASR as predicted by theory. ASR is an important moderator of selection promoting both adaptive behavioural plasticity and leading to the evolution of traits whose effects on an individual's fitness depend on patterns of mate availability.

(5) Through its effects on interactions between individuals that affect their fecundity or fertility, the ASR also affects demographic trends and population fitness, including the risk of local extinction. To understand fully the causes and consequences of ASR variation for sex roles, it is important to combine data from behavioural, population and evolutionary biology.

(6) Future studies should routinely report the ASR of the study population. The effects of ASR on behaviour may extend beyond those that define sex roles, and future studies could explore additional behavioural consequences of ASR variation, e.g. on success in intergroup conflict (Smith *et al.*, 2022) or collaborative hunting (Lang & Farine, 2017), as well as on physiological parameters such as immunocompetence (Stoehr & Kokko, 2006). We also lack an even basic understanding of the cognitive mechanisms used by individuals in different taxa to assess their local ratio of males to females. Humans appear to be very good at assessing the sex ratio of groups (e.g. Goodale *et al.*, 2018; Phillips, Slepian & Hughes, 2018). Finally, additional theoretical work on the links between sex ratios and sex roles in species with obligate uniparental care or lacking parental care would be welcome.

(7) We provide the first systematic review of the relationships between ASR and sex roles, but also social behaviour, physiology and fitness. We conclude that considering ASR in future studies of sexual selection and sex roles is an important aspect that deserves closer attention in empirical and theoretical research.

VI. ACKNOWLEDGEMENTS

VII. REFERENCES

Ah-King, M. (2012). On anisogamy and the evolution of "sex roles". *Trends in Ecology & Evolution* **28**, 1–2.

Ah-King, M. & Ahnesjö, I. (2013). The "sex role" concept: an overview and evaluation. *Evolutionary Biology* **40**, 461–470.

Ah-King, M. & Gowaty, P. A. (2016). A conceptual review of mate choice: stochastic demography, within-sex phenotypic plasticity, and individual flexibility. *Ecology and Evolution* **6**, 4607–4642.

Ahnesjö, I., Forsgren, E. & Kvarnemo, C. (2008). Variation in sexual selection. In *Fish Behaviour* (eds C. Magnhagen, V. A. Braithwaite, E. Forsgren and B. G. Kapoor), pp. 303–335. Science Publishers Inc., Enfield.

Aleuy, O. A., Serrano, E., Ruckstuhl, K. E., Hoberg, E. P. & Kutz, S. (2020). Parasite intensity drives fetal development and sex allocation in a wild ungulate. *Scientific Reports* **10**, 15626.

Alonzo, S. H. (2010). Social and coevolutionary feedbacks between mating and parental investment. *Trends in Ecology & Evolution* **25**, 99–108.

Amundsen, T. (2018). Sex roles and sexual selection: lessons from a dynamic model system. *Current Zoology* **64**, 363–392.

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

Ancona, S., Liker, A., Carmona-Isunza, M. C. & Székely, T. (2020). Sex differences in age-to-maturation relate to sexual selection and adult sex ratios in birds. *Evolution Letters* **4**, 44–53.

Andersson, M. (1994). *Sexual Selection*. Princeton University Press, Princeton.

Andersson, M. (1995). Evolution of reversed sex roles, sexual size dimorphism, and mating system in coucals (Centropodidae, Aves). *Biological Journal of the Linnean Society* **54**, 173–181.

Andersson, M. (2004). Social polyandry, parental investment, sexual selection, and evolution of reduced female gamete size. *Evolution* **58**, 24–34.

Andersson, M. (2005). Evolution of classical polyandry: three steps to female emancipation. *Ethology* **111**, 1–23.

Anthes, N., Häderer, I. K., Michiels, N. K. & Janicke, T. (2017). Measuring and interpreting sexual selection metrics: evaluation and guidelines. *Methods in Ecology and Evolution* **8**, 918–931.

Araya-Ajoy, Y. G., Dingemanse, N. J. & Kempenaers, B. (2016). Timing of extrapair fertilizations: within-pair fertilization trade-offs or pair synchrony spillovers? *Behavioral Ecology* **27**, 377–384.

Arnqvist, G. (1992a). Pre-copulatory fighting in a water strider; inter-sexual conflict or mate assessment? *Animal Behaviour* **43**, 559–567.

Arnqvist, G. (1992b). Spatial variation in selective regimes: sexual selection in the water strider, *Gerris odontogaster*. *Evolution* **46**, 914–929.

Arnqvist, G. (1992c). The effects of operational sex ratio on the relative mating success of extreme male phenotypes in the water strider *Gerris odontogaster* (Zett.) (Heteroptera; Gerridae). *Animal Behaviour* **43**, 681–683.

Arnqvist, G. & Rowe, L. (2005). *Sexual Conflict*. Princeton University Press, Princeton.

Aspbury, A. S., Grayson, K. L., Fantaye, S., Nichols, I., Myers-Burton, M., Ortiz-Mangual, X. & Gabor, C. R. (2017). The association between male-biased sex ratio and indicators of stress in red-spotted newts. *Physiology & Behavior* **173**, 156–162.

Bateman, A. J. (1948). Intrasexual selection in *Drosophila*. *Heredity* **2**, 349–368.

Bath, E., Edmunds, D., Norman, J., Atkins, C., Harper, L., Rostant, W. G., Chapman, T., Wigby, S. & Perry, J. C. (2021). Sex ratio and the evolution of aggression in fruit flies. *Proceedings of the Royal Society B: Biological Sciences* **288**, 20203053.

Bel-Venner, M. C., Dray, S., Allaine, D., Menu, F. & Venner, S. (2008). Unexpected male choosiness for mates in a spider. *Proceedings of the Royal Society B: Biological Sciences* **275**, 77–82.

Bentley, G. E., Wingfield, J. C., Morton, M. L. & Ball, G. F. (2000). Stimulatory effects on the reproductive axis in female songbirds by conspecific and heterospecific male song. *Hormones and Behavior* **37**, 179–189.

Berglund, A., Widemo, M. S. & Rosenqvist, G. (2005). Sex-role reversal revisited: choosy females and ornamented, competitive males in a pipefish. *Behavioral Ecology* **16**, 649–655.

Bonnet, X., Golubović, A., Arsovski, D., Đorđević, S., Ballouard, J.-M., Sterijovski, B., Ajtić, R., Barbraud, C. & Tomović, L. (2016). A prison effect in a wild population: a scarcity of females induces homosexual behaviors in males. *Behavioral Ecology* **27**, 1206–1215.

Borg, A. A., Forsgren, E. & Amundsen, T. (2006). Seasonal change in female choice for male size in the two-spotted goby. *Animal Behaviour* **72**, 763–771.

Bretman, A., Gage, M. J. G. & Chapman, T. (2011). Quick-change artists: male plastic behavioural responses to rivals. *Trends in Ecology & Evolution* **26**, 467–473.

Bro-Jørgensen, J. (2011). Intra- and intersexual conflicts and cooperation in the evolution of mating strategies: lessons learnt from ungulates. *Evolutionary Biology* **38**, 28–41.

Cade, W. H. & Souroukis, K. (1993). Reproductive competition and selection on male traits at varying sex ratios in the field cricket, *Gryllus pennsylvanicus*. *Behaviour* **126**, 45–62.

Cally, J. G., Stuart-Fox, D. & Holman, L. (2019). Meta-analytic evidence that sexual selection improves population fitness. *Nature Communications* **10**, 2017.

Campbell, C. J. (2006). Lethal intragroup aggression by adult male spider monkeys (*Ateles geoffroyi*). *American Journal of Primatology* **68**, 1197–1201.

Candolin, U. & Salesto, T. (2009). Does competition allow male mate choosiness in threespine sticklebacks? *The American Naturalist* **173**, 273–277.

Carmona-Isunza, M. C., Ancona, S., Szekely, T., Ramallo-Gonzalez, A. P., Cruz-Lopez, M., Serrano-Meneses, M. A. & Küpper, C. (2017). Adult sex ratio and operational sex ratio exhibit different temporal dynamics in the wild. *Behavioral Ecology* **28**, 523–532.

Charnov, E. (1982). *The Theory of Sex Allocation*. Princeton University Press, Princeton.

Cheney, D. L., Silk, J. B. & Seyfarth, R. M. (2012). Evidence for intrasexual selection in wild female baboons. *Animal Behaviour* **84**, 21–27.

Cheng, M.-F. (2003). Vocal self-stimulation: from the ring dove story to emotion-based vocal communication. *Advances in the Study of Behavior* **33**, 309–353.

Cheng, M.-F. (2008). The role of vocal self-stimulation in female responses to males: implications for state-reading. *Hormones and Behavior* **53**, 1–10.

Clark, L. & Grant, J. W. A. (2010). Intrasexual competition and courtship in female and male Japanese medaka, *Oryzias latipes*: effects of operational sex ratio and density. *Animal Behaviour* **80**, 707–712.

Clutton-Brock, T. H. (1991). *The Evolution of Parental Care*. Princeton University Press, Princeton.

Clutton-Brock, T. H. (2017). Reproductive competition and sexual selection. *Philosophical Transactions of the Royal Society B: Biological Sciences* **372**, 20160310.

Clutton-Brock, T. H. & Huchard, E. (2013). Social competition and selection in males and females. *Philosophical Transactions of the Royal Society B: Biological Sciences* **368**, 20130074.

Clutton-Brock, T. H. & Parker, G. A. (1992). Potential reproductive rates and the operation of sexual selection. *The Quarterly Review of Biology* **67**, 437–456.

Clutton-Brock, T. H. & Parker, G. A. (1995). Sexual coercion in animal societies. *Animal Behaviour* **49**, 1345–1365.

Clutton-Brock, T. H., Rose, K. E. & Guiness, F. E. (1997). Density-related changes in sexual selection in red deer. *Proceedings of the Royal Society B: Biological Sciences* **264**, 1509–1516.

Cordero, A. & Andrés, J. A. (2002). Male coercion and convenience polyandry in a calopterygid damselfly. *Journal of Insect Science* **2**, 14.

Courtiol, A., Etienne, L., Feron, R., Godelle, B. & Rousset, F. (2016). The evolution of mutual mate choice under direct benefits. *The American Naturalist* **188**, 521–538.

Cox, J. A., Cusick, J. A. & DuVal, E. H. (2019). Manipulated sex ratios alter group structure and cooperation in the brown-headed nuthatch. *Behavioral Ecology* **30**, 883–893.

Cureton, J. C., Martin, R. E. & Deaton, R. (2010). Short term changes in sex ratio and density alter coercive male mating tactics. *Behaviour* **147**, 1431–1442.

Dale, S. (2002). Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. *Oikos* **92**, 344–356.

Darden, S. K., James, R., Ramnarine, I. W. & Croft, D. P. (2009). Social implications of the battle of the sexes: sexual harassment disrupts female sociality and social recognition. *Proceedings of the Royal Society B: Biological Sciences* **276**, 2651–2656.

Darwin, C. (1871). *The Descent of Man and Selection in Relation to Sex*. Murray, London.

Davidian, E., Surbeck, M., Lukas, D., Kappeler, P. M. & Huchard, E. (2022). The eco-evolutionary landscape of power relationships between males and females. *Trends in Ecology & Evolution* **37**, 706–718.

de Jong, K., Forsgren, E., Sandvik, H. & Amundsen, T. (2012). Measuring mating competition correctly: available evidence supports operational sex ratio theory. *Behavioral Ecology* **23**, 1170–1177.

de Jong, K., Wacker, S., Amundsen, T. & Forsgren, E. (2009). Do operational sex ratio and density affect mating behaviour? An experiment on the two-spotted goby. *Animal Behaviour* **78**, 1229–1238.

Debuse, V. J., Addison, J. T. & Reynolds, J. D. (1999). The effects of sex ratio on sexual competition in the European lobster. *Animal Behaviour* **58**, 973–981.

delBarco-Trillo, J. (2011). Adjustment of sperm allocation under high risk of sperm competition across taxa: a meta-analysis. *Journal of Evolutionary Biology* **24**, 1706–1714.

Dewsbury, D. A. (2005). The Darwin-Bateman paradigm in historical context. *Integrative and Comparative Biology* **45**, 831–837.

Dhondt, A. A. & Adriaensen, F. (1994). Causes and effects of divorce in the blue tit *Parus caeruleus*. *Journal of Animal Ecology* **63**, 979–987.

Donald, P. (2007). Adult sex ratios in wild bird populations. *Ibis* **149**, 671–692.

Dougherty, L. R., Dewhurst, A. D. & Lewis, Z. (2020). Operational sex ratio does not influence the evolution of male mate choice in the Indian meal moth. *Journal of Ethology* **38**, 21–28.

Dufty, A. M. & Wingfield, J. C. (1986). The influence of social cues on the reproductive endocrinology of male brown-headed cowbirds: field and laboratory studies. *Hormones and Behavior* **20**, 222–234.

Düsing, C. (1884). Die Regulierung des Geschlechtsverhältnisses bei der Vermehrung der Menschen, Tiere und Pflanzen. *Jenaische Zeitschrift für Naturwissenschaft* **17**, 593–941.

Eberhart-Phillips, L. J., Küpper, C., Carmona-Isunza, M. C., Vincze, O., Zefania, S., Cruz-Lopez, M., Kosztolanyi, A., Miller, T. E. X., Barta, Z., Cuthill, I. C., Burke, T., Székely, T., Hoffman, J. I. & Krüger, O. (2018). Demographic causes of adult sex ratio variation and their consequences for parental cooperation. *Nature Communications* **9**, 1651.

Eberhart-Phillips, L. J., Küpper, C., Miller, T. E. X., Cruz-Lopez, M., Maher, K. H., Dos Remedios, N., Stoffel, M. A., Hoffmann, J. I., Krüger, O. & Székely, T. (2017). Sex-specific early survival drives adult sex ratio bias in snowy plovers and impacts mating system and population growth. *Proceedings of the National Academy of Sciences* **114**, E5474–E5481.

Edward, D. A. & Chapman, T. (2011). The evolution and significance of male mate choice. *Trends in Ecology & Evolution* **26**, 647–654.

Edward, D. A., Fricke, C. & Chapman, T. (2010). Adaptations to sexual selection and sexual conflict: insights from experimental evolution and artificial selection. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 2541–2548.

Edwards, A. W. F. (2000). Carl Düsing (1884) on the regulation of the sex-ratio. *Theoretical Population Biology* **58**, 255–257.

Emlen, S. T. (1976). Lek organization and mating strategies in the bullfrog. *Behavioral Ecology and Sociobiology* **1**, 283–313.

Emlen, S. T. & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science* **197**, 215–223.

Fedigan, L. M. & Jack, K. M. (2011). Two girls for every boy: the effects of group size and composition on the reproductive success of male and female white-faced capuchins. *American Journal of Physical Anthropology* **144**, 317–326.

Fisher, R. A. (1930). *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.

Fitze, P. S. & Le Galliard, J. (2008). Operational sex ratio, sexual conflict and the intensity of sexual selection. *Ecology Letters* **11**, 432–439.

Forsgren, E., Amundsen, T., Borg, A. A. & Bjelvenmark, J. (2004). Unusually dynamic sex roles in a fish. *Nature* **429**, 551–554.

Frasier, T. R., Hamilton, P. K., Brown, M. W., Conger, L. A., Knowlton, A. R., Marx, M. K., Slay, C. K., Kraus, S. D. & White, B. N. (2007). Patterns of male reproductive success in a highly promiscuous whale species: the endangered North Atlantic right whale. *Molecular Ecology* **16**, 5277–5293.

Fritzsche, K., Booksmythe, I. & Arnqvist, G. (2016). Sex ratio bias leads to the evolution of sex role reversal in honey locust beetles. *Current Biology* **26**, 2522–2526.

Fromhage, L. (2017). Parental care and investment. *eLS*. https://doi.org/10.1002/9780470015902.a0021907.pub2.

Fromhage, L. & Jennions, M. D. (2016). Coevolution of parental investment and sexually selected traits drives sex-role divergence. *Nature Communications* **7**, 12517.

Fromhage, L. & Jennions, M. D. (2017). Not all sex ratios are equal: the Fisher condition, parental care and sexual selection. *Philosophical Transactions of the Royal Society B: Biological Sciences* **372**, 20160312.

Gao, Y. & Kang, L. (2006). Operational sex ratio and alternative reproductive behaviours in Chinese bushcricket, *Gampsocleis gratiosa*. *Ethology* **112**, 325–331.

Garamszegi, L. Z., Eens, M., Hurtrez-Bousses, S. & Møller, A. P. (2005). Testosterone, testes size, and mating success in birds: a comparative study. *Hormones and Behavior* **47**, 389–409.

Godwin, J. L., Vasudeva, R., Michalczyk, Ł., Martin, O. Y., Lumley, A. J., Chapman, T. & Gage, M. J. G. (2017). Experimental evolution reveals that sperm competition intensity selects for longer, more costly sperm. *Evolution Letters* **1**, 102–113.

Goodale, B. M., Alt, N. P., Lick, D. J. & Johnson, K. L. (2018). Groups at a glance: perceivers infer social belonging in a group based on perceptual summaries of sex ratio. *Journal of Experimental Psychology: General* **147**, 1660–1676.

Gowaty, P. A. (2004). Sex roles, contests for the control of reproduction, and sexual selection. In *Sexual Selection in Primates: New and Comparative Perspectives* (eds P. M. Kappeler and C. P. van Schaik), pp. 37–54. Cambridge University Press, Cambridge.

Gowaty, P. A., Kim, Y.-K. & Anderson, W. W. (2012). No evidence of sexual selection in a repetition of Bateman's classic study of *Drosophila melanogaster*. *Proceedings of the National Academy of Sciences of the United States of America* **109**, 11740–11745.

GOYMANN, W., EAST, M. L. & HOFER, H. (2003). Defense of females, but not social status, predicts plasma androgen levels in male spotted hyenas. *Physiological and Biochemical Zoology* **76**, 586–593.

GOYMANN, W. & FLORES DÁVILA, P. (2017). Acute peaks of testosterone suppress paternal care: evidence from individual hormonal reaction norms. *Proceedings of the Royal Society B: Biological Sciences* **284**, 20170632.

GOYMANN, W., MAKOMBA, M., URASA, F. & SCHWABL, I. (2015). Social monogamy vs. polyandry: ecological factors associated with sex roles in two closely related birds within the same habitat. *Journal of Evolutionary Biology* **28**, 1335–1353.

GOYMANN, W., MOORE, I. T. & OLIVEIRA, R. F. (2019). Challenge hypothesis 2.0: a fresh look at an established idea. *Bioscience* **69**, 432–442.

GOYMANN, W., WITTENZELLNER, A., SCHWABL, I. & MAKOMBA, M. (2008). Progesterone modulates aggression in sex-role reversed African black coucals. *Proceedings of the Royal Society of B: Biological Sciences* **275**, 1053–1060.

GRANT, J. W. & FOAM, P. E. (2002). Effect of operational sex ratio on female female versus male male competitive aggression. *Canadian Journal of Zoology* **80**, 2242–2246.

GRANT, P. R. & GRANT, B. R. (2019). Adult sex ratio influences mate choice in Darwin's finches. *Proceedings of the National Academy of Sciences of the United States of America* **116**, 12373–12382.

HAMILTON, W. D. (1967). Extraordinary sex ratios. *Science* **156**, 477.

HARE, R. M. & SIMMONS, L. W. (2019). Sexual selection and its evolutionary consequences in female animals. *Biological Reviews* **94**, 929–956.

HARTS, A. M. & KOKKO, H. (2013). Understanding promiscuity: when is seeking additional mates better than guarding an already found one? *Evolution* **67**, 2838–2848.

HEAD, M. L., LINDHOLM, A. K. & BROOKS, R. (2008). Operational sex ratio and density do not affect directional selection on male sexual ornaments and behavior. *Evolution* **62**, 135–144.

HEIMERL, D., DUDOVÁ, P., WACKER, K., SCHENKEL, E., DESPRÉAUX, G. & TUNI, C. (2022). Adult sex ratio and male body condition affect alternative reproductive tactics in a spider. *Behavioral Ecology* **33**, 271–279.

HEINSOHN, R., OLAH, G., WEBB, M., PEAKALL, R. & STOJANOVIC, D. (2019). Sex ratio bias and shared paternity reduce individual fitness and population viability in a critically endangered parrot. *Journal of Animal Ecology* **88**, 502–510.

HEMELRIJK, C. K. & LUTEIJN, M. (1998). Philopatry, male presence and grooming reciprocation among female primates: a comparative perspective. *Behavioral Ecology and Sociobiology* **42**, 207–215.

HEMELRIJK, C. K., WANTIA, J. & ISLER, K. (2008). Female dominance over males in primates: self-organisation and sexual dimorphism. *PLoS One* **3**, e2678.

HIRSCHENHAUSER, K., GAHR, M. & GOYMANN, W. (2013). Winning and losing in public: audiences direct future success in Japanese quail. *Hormones and Behavior* **63**, 625–633.

HOLVECK, M.-J., GAUTHIER, A.-L. & NIEBERDING, C. M. (2015). Dense, small and male-biased cages exacerbate male–male competition and reduce female choosiness in *Bicyclus anynana*. *Animal Behaviour* **104**, 229–245.

HOPKINS, B. R., SEPIL, I., THÉZÉNAS, M.-L., CRAIG, J. F., MILLER, T., CHARLES, P. D., FISCHER, R., KESSLER, B. M., BRETMAN, A. & PIZZARI, T. (2019). Divergent allocation of sperm and the seminal proteome along a competition gradient in *Drosophila melanogaster*. *Proceedings of the National Academy of Sciences of the United States of America* **116**, 17925–17933.

HOQUET, T. (2020). Bateman (1948): rise and fall of a paradigm? *Animal Behaviour* **164**, 223–231.

HOUSTON, A. I. & MCNAMARA, J. M. (2002). A self-consistent approach to paternity and parental effort. *Philosophical Transactions of the Royal Society B: Biological Sciences* **357**, 351–362.

HUCK, M., FERNANDEZ-DUQUE, E., BABB, P. & SCHURR, T. (2014). Correlates of genetic monogamy in socially monogamous mammals: insights from Azara's owl monkeys. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20140195.

INGLEBY, F. C., LEWIS, Z. & WEDELL, N. (2010). Level of sperm competition promotes evolution of male ejaculate allocation patterns in a moth. *Animal Behaviour* **80**, 37–43.

JANICKE, T., DAVID, P. & CHAPUIS, E. (2015). Environment-dependent sexual selection: Bateman's parameters under varying levels of food availability. *The American Naturalist* **185**, 756–768.

JANICKE, T. & FROMONTEIL, S. (2021). Sexual selection and sexual size dimorphism in animals. *Biology Letters* **17**, 20210251.

JANICKE, T., HÄDERER, I. K., LAJEUNESSE, M. J. & ANTHES, N. (2016). Darwinian sex roles confirmed across the animal kingdom. *Science Advances* **2**, e1500983.

JANICKE, T. & MORROW, E. H. (2018). Operational sex ratio predicts the opportunity and direction of sexual selection across animals. *Ecology Letters* **21**, 384–391.

JEHAN, C., CHOGNE, M., RIGAUD, T. & MORET, Y. (2020). Sex-specific patterns of senescence in artificial insect populations varying in sex-ratio to manipulate reproductive effort. *BMC Evolutionary Biology* **20**, 18.

JENNIONS, M. D. & FROMHAGE, L. (2017). Not all sex ratios are equal: the Fisher condition, parental care and sexual selection. *Philosophical Transactions of the Royal Society B: Biological Sciences* **372**, 20160312.

JENNIONS, M. D. & KOKKO, H. (2010). Sexual selection. In *Evolutionary Behavioral Ecology* (eds D. WESTNEAT and C. FOX), pp. 343–364. Oxford University Press, New York.

JENNIONS, M. D., SZÉKELY, T., BEISSINGER, S. R. & KAPPELER, P. M. (2017). Sex ratios. *Current Biology* **27**, R790–R792.

JIROTKUL, M. (1999). Operational sex ratio influences female preference and male-male competition in guppies. *Animal Behaviour* **58**, 287–294.

JOHANOS, T. C., BECKER, B. L., BAKER, J. D., RAGEN, T. J., GILMARTIN, W. G. & GERRODETTE, T. (2010). Impacts of sex ratio reduction on male aggression in the critically endangered Hawaiian monk seal *Monachus schauinslandi*. *Endangered Species Research* **11**, 123–132.

KAHN, J. E., WATTERSON, J. C., HAGER, C. H., MATHIES, N. & HARTMAN, K. J. (2021). Calculating adult sex ratios from observed breeding sex ratios for wide-ranging, intermittently breeding species. *Ecosphere* **12**, e03504.

KALMBACH, E. & BENITO, M. M. (2007). Sexual size dimorphism and offspring vulnerability in birds. In *Sex, Size and Gender Roles. Evolution of Sexual Size Dimorphism* (eds D. J. FAIRBAIRN, W. U. BLANCKENHORN and T. SZÉKELY), pp. 133–142. Oxford University Press, Oxford.

KAPPELER, P. M. (2013). Why male mammals are monogamous. *Science* **341**, 469–470.

KAPPELER, P. M. (2017). Sex roles and adult sex ratios: insights from mammalian biology and consequences for primate behaviour. *Philosophical Transactions of the Royal Society B: Biological Sciences* **372**, 20160321.

KAPPELER, P. M. (2019). A framework for studying social complexity. *Behavioral Ecology and Sociobiology* **73**, 13.

KAPPELER, P. M. & FICHTEL, C. (2012). A 15-year perspective on the social organization and life history of sifaka in Kirindy Forest. In *Long-Term Field Studies of Primates* (eds P. M. KAPPELER and D. P. WATTS), pp. 101–121. Springer, Heidelberg.

KAPPELER, P. M., VAN SCHAIK, C. P. & WATTS, D. P. (2012). The values and challenges of long-term field studies. In *Long-Term Field Studies of Primates* (eds P. M. KAPPELER and D. P. WATTS), pp. 3–18. Springer, Heidelberg.

KAPPUS, S. & FONG, P. (2014). Sex ratio does not influence sex change despite its effect on reproductive success. *Behavioral Ecology* **25**, 827–833.

KEENLEYSIDE, M. H. A. (1983). Mate desertion in relation to adult sex ratio in the biparental cichlid fish *Herotilapia multispinosa*. *Animal Behaviour* **31**, 683–688.

KELLY, C. D. (2015). Male-biased sex ratios and plasticity in post-insemination behaviour in the New Zealand stick insect *Micrarchus hystriculeus*. *Behaviour* **152**, 653–666.

KELLY, C. D. & JENNIONS, M. D. (2011). Sexual selection and sperm quantity: meta-analyses of strategic ejaculation. *Biological Reviews* **86**, 863–884.

KEMPENAERS, B. (1994). Polygyny in the blue tit: unbalanced sex ratio and female aggression restrict mate choice. *Animal Behaviour* **47**, 943–957.

KERTH, G. & VAN SCHAIK, J. (2012). Causes and consequences of living in closed societies: lessons from a long-term socio-genetic study on Bechstein's bats. *Molecular Ecology* **21**, 633–646.

KHAN, I., PRAKASH, A., ISSAR, S., UMARANI, M., SASIDHARAN, R., MASAGALLI, J. N., LAMA, P., VENKATESAN, R. & AGASHE, D. (2018). Female density-dependent chemical warfare underlies fitness effects of group sex ratio in flour beetles. *The American Naturalist* **191**, 306–317.

KHIDR, S. K., MAYES, S. & HARDY, I. C. W. (2013). Primary and secondary sex ratios in a gregarious parasitoid with local mate competition. *Behavioral Ecology* **24**, 435–443.

KLUG, H., BONSALL, M. B. & ALONZO, S. H. (2013). The origin of parental care in relation to male and female life history. *Ecology and Evolution* **3**, 779–791.

KOKKO, H., BOOKSMYTHE, I. & JENNIONS, M. D. (2013). Causality and sex roles: prejudice against patterns? A reply to Ah-King. *Trends in Ecology & Evolution* **28**, 2–4.

KOKKO, H., BROOKS, R., JENNIONS, M. D. & MORLEY, J. (2003). The evolution of mate choice and mating biases. *Proceedings of the Royal Society B: Biological Sciences* **270**, 653–664.

KOKKO, H. & JENNIONS, M. D. (2008). Parental investment, sexual selection and sex ratios. *Journal of Evolutionary Biology* **21**, 919–948.

KOKKO, H. & JENNIONS, M. D. (2014). The relationship between sexual selection and sexual conflict. *Cold Spring Harbor Perspectives in Biology* **6**, a017517.

KOKKO, H. & JOHNSTONE, R. A. (2002). Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signalling. *Philosophical Transactions of the Royal Society B: Biological Sciences* **357**, 319–330.

KOKKO, H., KLUG, H. & JENNIONS, M. D. (2012). Unifying cornerstones of sexual selection: operational sex ratio, Bateman gradient and the scope for competitive investment. *Ecology Letters* **15**, 1340–1351.

KOMDEUR, J. (2012). Sex allocation. In *The Evolution of Parental Care* (eds N. J. ROYLE, P. T. SMISETH and M. KÖLLIKER), pp. 171–188. Oxford University Press, Oxford.

KOSZTOLÁNYI, A., BARTA, Z., KÜPPER, C. & SZÉKELY, T. (2011). Persistence of an extreme male-biased adult sex ratio in a natural population of polyandrous bird. *Journal of Evolutionary Biology* **24**, 1842–1846.

KVARNEMO, C. (2018). Why do some animals mate with one partner rather than many? A review of causes and consequences of monogamy. *Biological Reviews* **93**, 1795–1812.

Kvarnemo, C. & Ahnesjö, I. (1996). The dynamics of operation sex ratios and competition for mates. *Trends in Ecology & Evolution* 11, 404–408.

Kvarnemo, C., Forsgren, E. & Magnhagen, C. (1995). Effects of sex ratio on intra-and inter-sexual behaviour in sand gobies. *Animal Behaviour* 50, 1455–1461.

Kvarnemo, C. & Simmons, L. W. (2013). Polyandry as a mediator of sexual selection before and after mating. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368, 20120042.

Lang, S. D. J. & Farine, D. R. (2017). A multidimensional framework for studying social predation strategies. *Nature Ecology & Evolution* 1, 1230–1239.

Le Galliard, J.-F., Fitze, P. S., Ferrière, R. & Clobert, J. (2005). Sex ratio bias, male aggression, and population collapse in lizards. *Proceedings of the National Academy of Sciences of the United States of America* 102, 18231–18236.

Lessells, C. M. (1999). Sexual conflict in animals. In *Levels of Selection in Evolution* (ed. L. Keller), pp. 73–99. Princeton University Press, Princeton.

Lessells, C. M. (2012). Sexual conflict. In *The Evolution of Parental Care* (eds N. P. Royle, P. T. Smiseth and M. Kölliker), pp. 150–170. Oxford University Press, Oxford.

Liao, C., Yu, D., Chen, Y., Reichard, M. & Liu, H. (2014). Reproductive behaviour of female rosy bitterling *Rhodeus ocellatus* in response to a female-biased operational sex ratio. *Behaviour* 151, 755–768.

Ligon, J. D. (1993). The role of phylogenetic history in the evolution of contemporary avian mating and parental care systems. *Current Ornithology* 10, 1–46.

Ligon, J. D. (1999). *The Evolution of Avian Breeding Systems*. Oxford University Press, Oxford.

Liker, A., Bókony, V., Pipoly, I., Lemaître, J. F., Galliard, J. M., Székely, T. & Freckleton, R. P. (2021). Evolution of large males is associated with female-skewed adult sex ratios in amniotes. *Evolution* 75, 1636–1649.

Liker, A., Freckleton, R. P. & Székely, T. (2013). The evolution of sex roles in birds is related to adult sex ratio. *Nature Communications* 4, 1587.

Liker, A., Freckleton, R. P. & Székely, T. (2014). Divorce and infidelity are associated with skewed adult sex ratios in birds. *Current Biology* 24, 880–884.

Linklater, J. R., Wertheim, B., Wigby, S. & Chapman, T. (2007). Ejaculate depletion patterns evolve in response to experimental manipulation of sex ratio in *Drosophila melanogaster*. *Evolution* 61, 2027–2034.

Lodé, T. (2009). For a few males more: do changes in sex ratio predict reproductive success and offspring survival? *Evolutionary Ecology Research* 11, 95–107.

Lodé, T., Holveck, M. J. & Lesbarreres, D. (2005). Asynchronous arrival pattern, operational sex ratio and occurrence of multiple paternities in a territorial breeding anuran, *Rana dalmatina*. *Biological Journal of the Linnean Society* 86, 191–200.

Lodé, T., Holveck, M. J., Lesbarreres, D. & Pagano, A. (2004). Sex-biased predation by polecats influences the mating system of frogs. *Proceedings of the Royal Society B: Biological Sciences* 271, S399–S401.

Løvlie, H. & Pizzari, T. (2007). Sex in the morning or in the evening? Females adjust daily mating patterns to the intensity of sexual harassment. *The American Naturalist* 170, E1–E13.

Lynch, K. S., Azieva, G. & Pellicano, A. (2018). Socially regulated estrogen in an eavesdropping brood parasite. *General and Comparative Endocrinology* 269, 166–170.

Maan, M. E. & Taborsky, M. (2008). Sexual conflict over breeding substrate causes female expulsion and offspring loss in a cichlid fish. *Behavioral Ecology* 19, 302–308.

Magrath, M. J. L. & Elgar, M. A. (1997). Paternal care declines with increased opportunity for extra-pair matings in fairy martins. *Proceedings of the Royal Society B: Biological Sciences* 264, 1731–1736.

Magris, M. (2021). Strategic adjustment of ejaculate quality in response to variation of the socio-sexual environment. *Behavioral Ecology and Sociobiology* 75, 91.

Mathews, L. M. (2002). Tests of the mate-guarding hypothesis for social monogamy: does population density, sex ratio, or female synchrony affect behavior of male snapping shrimp (*Alpheus angulatus*)? *Behavioral Ecology and Sociobiology* 51, 426–432.

Mayr, E. (1939). The sex ratio in wild birds. *The American Naturalist* 73, 156–179.

McNamara, J. M., Székely, T., Webb, J. N. & Houston, A. I. (2000). A dynamic game theoretic model of parental care. *Journal of Theoretical Biology* 205, 605–623.

McNamara, K. B., Dougherty, L. R., Wedell, N. & Simmons, L. W. (2019). Experimental evolution reveals divergence in female genital teeth morphology in response to sexual conflict intensity in a moth. *Journal of Evolutionary Biology* 32, 519–524.

McNamara, K. B., Sloan, N. S., Kershaw, S. E., Van Lieshout, E. & Simmons, L. W. (2020). Males evolve to be more harmful under increased sexual conflict intensity in a seed beetle. *Behavioral Ecology* 31, 591–597.

McNamara, K. B., Wedell, N. & Simmons, L. W. (2013). Experimental evolution reveals trade-offs between mating and immunity. *Biology Letters* 9, 20130262.

Michalczyk, Ł., Millard, A. L., Martin, O. Y., Lumley, A. J., Emerson, B. C. & Gage, M. J. (2011). Experimental evolution exposes female and male responses to sexual selection and conflict in *Tribolium castaneum*. *Evolution* 65, 713–724.

Michener, G. R. & McLean, I. G. (1996). Reproductive behaviour and operational sex ratio in Richardson's ground squirrels. *Animal Behaviour* 52, 743–758.

Miller, S. L., Maner, J. K. & McNulty, J. K. (2012). Adaptive attunement to the sex of individuals at a competition: the ratio of opposite- to same-sex individuals correlates with changes in competitors' testosterone levels. *Evolution and Human Behavior* 33, 57–63.

Mills, S. C. & Reynolds, J. D. (2003). Operational sex ratio and alternative reproductive behaviours in the European bitterling, *Rhodeus sericeus*. *Behavioral Ecology and Sociobiology* 54, 98–104.

Mokos, J., Scheuring, I., Liker, A., Freckleton, R. P. & Székely, T. (2021). Degree of anisogamy is unrelated to the intensity of sexual selection. *Scientific Reports* 11, 19424.

Moore, I. T., Hernandez, J. & Goymann, W. (2020). Who rises to the challenge? Testing the Challenge Hypothesis in fish, amphibians, reptiles, and mammals. *Hormones and Behavior* 123, 104537.

Morimoto, J. (2020). Bateman (1948): was it all wrong? A comment on Hoquet (2020). *Animal Behaviour* 168, e1–e4.

Neuhoff, J. G. (2017). The perception of operational sex ratios by voice. *Scientific Reports* 7, 17754.

Noë, R. (2017). Local mating markets in humans and non-human animals. *Behavioral Ecology and Sociobiology* 71, 148.

Orzack, S. H., Stubblefield, J. W., Akmaev, V. R., Colls, P., Munné, S., Scholl, T., Steinsaltz, D. & Zuckerman, J. E. (2015). The human sex ratio from conception to birth. *Proceedings of the National Academy of Sciences of the United States of America* 112, E2102–E2111.

Owens, I. P. & Bennett, P. M. (1997). Variation in mating system among birds: ecological basis revealed by hierarchical comparative analysis of mate desertion. *Proceedings of the Royal Society B: Biological Sciences* 264, 1103–1110.

Parker, G. A. (2006). Sexual conflict over mating and fertilization: an overview. *Philosophical Transactions of the Royal Society B: Biological Sciences* 361, 235–259.

Parker, G. A. (2014). The sexual cascade and the rise of pre-ejaculatory (Darwinian) sexual selection, sex roles, and sexual conflict. *Cold Spring Harbor Perspectives in Biology* 6, a017509.

Parker, G. A., Baker, R. R. & Smith, V. G. F. (1972). The origin and evolution of gamete dimorphism and the male-female phenomenon. *Journal of Theoretical Biology* 36, 529–553.

Parker, G. A. & Simmons, L. W. (1996). Parental investment and the control of sexual selection: predicting the direction of sexual competition. *Proceedings of the Royal Society of London B* 263, 315–321.

Parker, G. A., Simmons, L. W. & Kirk, H. (1990). Analysing sperm competition data: simple models for predicting mechanisms. *Behavioral Ecology and Sociobiology* 27, 55–65.

Parra, J. E., Beltran, M., Zefania, S., dos Remedios, N. & Szekely, T. (2014). Experimental assessment of mating opportunities in three shorebird species. *Animal Behaviour* 90, 83–90.

Phillips, L. T., Slepian, M. L. & Hughes, B. L. (2018). Perceiving groups: the people perception of diversity and hierarchy. *Journal of Personality and Social Psychology* 114, 766–785.

Pilastro, A., Biddau, L., Marin, G. & Mingozzi, T. (2001). Female brood desertion increases with number of available mates in the rock sparrow. *Journal of Avian Biology* 32, 68–72.

Pinxten, R., de Ridder, E. & Eens, M. (2003). Female presence affects male behavior and testosterone levels in the European starling (*Sturnus vulgaris*). *Hormones and Behavior* 44, 103–109.

Pollo, P. & Kasumovic, M. M. (2022). Let's talk about sex roles: what affects perceptions of sex differences in animal behaviour? *Animal Behaviour* 183, 1–12.

Port, M., Kappeler, P. M. & Johnstone, R. A. (2011). Communal defense of territories and the evolution of sociality. *The American Naturalist* 178, 787–800.

Prohl, H. (2002). Population differences in female resource abundance, adult sex ratio, and male mating success in *Dendrobates pumilio*. *Behavioral Ecology* 13, 175–181.

Queller, D. C. (1997). Why do females care more than males? *Proceedings of the Royal Society B: Biological Sciences* 264, 1555–1557.

Rankin, D. J. & Kokko, H. (2007). Do males matter? The role of males in population dynamics. *Oikos* 116, 335–348.

Regan, C. E., Medill, S. A., Poissant, J. & McLoughlin, P. D. (2020). Causes and consequences of an unusually male-biased adult sex ratio in an unmanaged feral horse population. *Journal of Animal Ecology* 89, 2909–2921.

Reuter, M., Linklater, J. R., Lehmann, L., Fowler, K., Chapman, T. & Hurst, G. D. D. (2008). Adaptation to experimental alterations of the operational sex ratio in populations of *Drosophila melanogaster*. *Evolution* 62, 401–412.

Rosa, M. E., Barta, Z., Fülöp, A., Székely, T. & Kosztolányi, A. (2017). The effects of adult sex ratio and density on parental care in *Lethrus apterus* (Coleoptera, Geotrupidae). *Animal Behaviour* 132, 181–188.

Rosenbaum, S., Maldonado-Chaparro, A. A. & Stoinski, T. S. (2016). Group structure predicts variation in proximity relationships between male–female and male–infant pairs of mountain gorillas (*Gorilla beringei beringei*). *Primates* 57, 17–28.

Rossi, B. H., Nonacs, P. & Pitts-Singer, T. L. (2010). Sexual harassment by males reduces female fecundity in the alfalfa leafcutting bee, *Megachile rotundata*. *Animal Behaviour* 79, 165–171.

ROUGHGARDEN, J., OISHI, M. & AKCAY, E. (2006). Reproductive social behavior: cooperative games to replace sexual selection. *Science* **311**, 965–969.

SAFARI, I. & GOYMANN, W. (2021). The evolution of reversed sex roles and classical polyandry: insights from coucals and other animals. *Ethology* **127**, 1–13.

SAFARI, I., GOYMANN, W. & KOKKO, H. (2019). Male-only care and cuckoldry in black coucals: does parenting hamper sex life? *Proceedings of the Royal Society B: Biological Sciences* **286**, 20182789.

SAPOLSKY, R. M. & SHARE, L. J. (2004). A pacific culture among wild baboons: its emergence and transmission. *PLoS Biology* **2**, 534–541.

SCHACHT, R., BEISSINGER, S. R., WEDEKIND, C., JENNIONS, M. J., GEFFROY, B., LIKER, A., KAPPELER, P. M., WEISSING, F. J., KRAMER, K. L., HESKETH, T., BOISSIER, J., UGGLA, C., HOLLINGSHAUS, M. & SZÉKELY, T. (in press). Adult sex ratios: causes of variation and implications for animal and human societies. *Communications Biology*.

SCHÄRER, L., ROWE, L. & ARNQVIST, G. (2012). Anisogamy, chance and the evolution of sex roles. *Trends in Ecology & Evolution* **27**, 260–264.

SCHÖFL, G. & TABORSKY, M. (2002). Prolonged tandem formation in firebugs (*Pyrrhocoris apterus*) serves mate-guarding. *Behavioral Ecology and Sociobiology* **52**, 426–433.

SCHRADIN, C., DROUARD, F., LEMONNIER, G., ASKEW, R., OLIVIER, C. A. & PILLAY, N. (2020). Geographic intra-specific variation in social organization is driven by population density. *Behavioral Ecology and Sociobiology* **74**, 113.

SCHWAGMEYER, P. L., MOCK, D. W. & BARTLETT, T. L. (2016). Chronically time-in or intermittently time-out? Differentiating time-out from a shortage of opportunities. *Animal Behaviour* **111**, 281–288.

SHINE, R., LANGKILDE, T. & MASON, R. T. (2003). The opportunistic serpent: male garter snakes adjust courtship tactics to mating opportunities. *Behaviour* **140**, 1509–1526.

SIMMONS, L. W. (2001). *Sperm Competition and its Evolutionary Consequences in the Insects*. Princeton University Press, Princeton.

SIMMONS, L. W. & GWYNNE, D. T. (1993). Reproductive investment in bushcrickets: the allocation of male and female nutrients to offspring. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **252**, 1–5.

SMITH, C. C. (2007). Independent effects of male and female density on sexual harassment, female fitness, and male competition for mates in the western mosquitofish *Gambusia affinis*. *Behavioral Ecology and Sociobiology* **61**, 1349–1358.

SMITH, J., FICHTEL, C., HOLMES, R., KAPPELER, P. M., VAN VUGT, M. & JAEGGI, A. (2022). Sex bias in intergroup conflict and collective movements among social mammals: male warriors and female guides. *Philosophical Transactions of the Royal Society B: Biological Sciences* **377**, 20210142.

SMUTS, B. B. & SMUTS, R. W. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Advances in the Study of Behavior* **22**, 1–63.

SOUROUKIS, K. & MURRAY, A.-M. (1995). Female mating behavior in the field cricket, *Gryllus pennsylvanicus* (Orthoptera, Gryllidae) at different operational sex ratios. *Journal of Insect Behavior* **8**, 269–279.

SOWERSBY, W., GONZALEZ-VOYER, A. & ROGELL, B. (2020). Sex ratios deviate across killifish species without clear links to life history. *Evolutionary Ecology* **34**, 411–426.

STOCKLEY, P. & CAMPBELL, A. (2013). Female competition and aggression: interdisciplinary perspectives. *Philosophical Transactions of the Royal Society B: Biological Sciences* **368**, 20130073.

STOEHR, A. M. & KOKKO, H. (2006). Sexual dimorphism in immunocompetence: what does life-history theory predict? *Behavioral Ecology* **17**, 751–756.

STUMPF, R. M. & BOESCH, C. (2010). Male aggression and sexual coercion in wild West African chimpanzees, *Pan troglodytes verus*. *Animal Behaviour* **79**, 333–342.

SUTHERLAND, W. J. (1985). Chance can produce a sex difference in variance in mating success and explain Bateman's data. *Animal Behaviour* **33**, 1349–1352.

SZÉKELY, T., LIKER, A., FRECKLETON, R. P., FICHTEL, C. & KAPPELER, P. M. (2014a). Sex-biased survival predicts adult sex ratio variation in wild birds. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20140342.

SZÉKELY, T., WEBB, J. N. & CUTHILL, I. C. (2000). Mating patterns, sexual selection and parental care: an integrative approach. In *Vertebrate Mating Systems* (eds M. APOLLONIO, M. FESTA-BIANCHET and D. MAINARDI), pp. 194–223. World Scientific Press, Singapore.

SZÉKELY, T., WEISSING, F. J. & KOMDEUR, J. (2014b). Adult sex ratio variation: implications for breeding system evolution. *Journal of Evolutionary Biology* **27**, 1500–1512.

TRIVERS, R. L. (1972). Parental investment and sexual selection. In *Sexual Selection and the Descent of Man* (ed. B. CAMPBELL), pp. 136–179. Aldine Press, Chicago.

TRIVERS, R. L. & WILLARD, D. E. (1973). Natural selection of parental ability to vary the sex ratio of offspring. *Science* **179**, 90–92.

VAN LIESHOUT, E., MCNAMARA, K. B. & SIMMONS, L. W. (2014). Rapid loss of behavioral plasticity and immunocompetence under intense sexual selection. *Evolution* **68**, 2550–2558.

VERAN, S. & BEISSINGER, S. R. (2009). Demographic origins of skewed operational and adult sex ratios: perturbation analyses of two-sex models. *Ecology Letters* **12**, 129–143.

VINCENT, A., AHNESJÖ, I., BERGLUND, A. & ROSENQVIST, G. (1992). Pipefishes and seahorses: are they all sex role reversed? *Trends in Ecology & Evolution* **7**, 237–241.

VRTÍLEK, M., ZÁK, J., POLACIK, M., BLAZEK, R. & REICHARD, M. (2018). Longitudinal demographic study of wild populations of African annual killifish. *Scientific Reports* **8**, 4774.

VULLIOUD, C., DAVIDIAN, E., WACHTER, B., ROUSSET, F., COURTIOL, A. & HÖNER, O. P. (2019). Social support drives female dominance in the spotted hyaena. *Nature Ecology & Evolution* **3**, 71–76.

WACKER, S., MOBLEY, K., FORSGREN, E., MYHRE, L. C., DE JONG, K. & AMUNDSEN, T. (2013). Operational sex ratio but not density affects sexual selection in a fish. *Evolution* **67**, 1937–1949.

WATTS, H. E., EDLEY, B. & HAHN, T. P. (2016). A potential mate influences reproductive development in female, but not male, pine siskins. *Hormones and Behavior* **80**, 39–46.

WAYNE, A. F., MAXWELL, M. A., WARD, C. G., VELLIOS, C. V., WILSON, I., WAYNE, J. C. & WILLIAMS, M. R. (2015). Sudden and rapid decline of the abundant marsupial *Bettongia penicillata* in Australia. *Oryx* **49**, 175–185.

WEBB, J. N., HOUSTON, A. I., MCNAMARA, J. M. & SZEKELY, T. (1999). Multiple patterns of parental care. *Animal Behaviour* **58**, 983–993.

WEDEKIND, C. (2017). Demographic and genetic consequences of disturbed sex determination. *Philosophical Transactions of the Royal Society B: Biological Sciences* **372**, 20160326.

WEIR, L. K. (2013). Male–male competition and alternative male mating tactics influence female behavior and fertility in Japanese medaka (*Oryzias latipes*). *Behavioral Ecology and Sociobiology* **67**, 193–203.

WEIR, L. K., GRANT, J. W. A. & HUTCHINGS, J. A. (2011). The influence of operational sex ratio on the intensity of competition for mates. *The American Naturalist* **177**, 167–176.

WEST, H. E. & CAPELLINI, I. (2016). Male care and life history traits in mammals. *Nature Communications* **7**, 11854.

WEST, S. A. (2009). *Sex Allocation*. Princeton University Press, Princeton.

WHITEHEAD, H., ANTUNES, R., GERO, S., WONG, S. N., ENGELHAUPT, D. & RENDELL, L. (2012). Multilevel societies of female sper whales (*Physeter macrocephalus*) in the Atlantic and Pacific: why are they so different? *International Journal of Primatology* **33**, 1142–1164.

WIGBY, S., BROWN, N. C., ALLEN, S. E., MISRA, S., SITNIK, J. L., SEPIL, I., CLARK, A. G. & WOLFNER, M. F. (2020). The *Drosophila* seminal proteome and its role in postcopulatory sexual selection. *Philosophical Transactions of the Royal Society B: Biological Sciences* **375**, 20200072.

WIGBY, S. & CHAPMAN, T. (2004). Female resistance to male harm evolves in response to manipulation of sexual conflict. *Evolution* **58**, 1028–1037.

WINGFIELD, J. C., HEGNER, R. E., DUFTY, A. M. & BALL, G. F. (1990). The "challenge hypothesis": theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *The American Naturalist* **136**, 829–846.

WINGFIELD, J. C., MOORE, I. T., GOYMANN, W., WACKER, D. & SPERRY, T. (2006). Contexts and ethology of vertebrate aggression: implications for the evolution of hormone-behavior interactions. In *Biology of Aggression* (ed. R. NELSON), pp. 179–210. Oxford University Press, New York.

WINGFIELD, J. C., NEWMAN, A. L., HUNT, G. L. & FARNER, D. S. (1982). Endocrine aspects of female-female pairing in the western gull (*Larus occidentalis wymani*). *Animal Behaviour* **30**, 9–22.

WITTEMYER, G., DOUGLAS-HAMILTON, I. & GETZ, W. M. (2005). The socioecology of elephants: analysis of the processes creating multitiered social structures. *Animal Behaviour* **69**, 1357–1371.

YAMAMURA, N. & TSUJI, N. (1993). Parental care as a game. *Journal of Evolutionary Biology* **6**, 103–127.

ZACK, S. & STUTCHBURY, B. J. (1992). Delayed breeding in avian social systems: the role of territory quality and "floater" tactics. *Behaviour* **123**, 194–219.

ZHENG, J., KOMDEUR, J., SZÉKELY, T., VERSTEEGH, M. A., LI, D., WANG, H. & ZHANG, Z. (2021). Males and females of a polygamous songbird respond differently to mating opportunities. *Behavioral Ecology and Sociobiology* **75**, 72.

ZIMMERMANN, T. D., KAISER, S., HENNESSY, M. B. & SACHSER, N. (2017). Adaptive shaping of the behavioural and neuroendocrine phenotype during adolescence. *Proceedings of the Royal Society B: Biological Sciences* **284**, 20162784.