JOURNAL OF Evolutionary Biology

doi: 10.1111/jeb.12415

REVIEW

Adult sex ratio variation: implications for breeding system evolution

T. SZÉKELY*†‡, F. J. WEISSING† & J. KOMDEUR‡

*Biodiversity Lab, Department of Biology & Biochemistry, University of Bath, Bath, UK
†Theoretical Biology, Centre for Ecological and Evolutionary Studies, University of Groningen, Groningen, The Netherlands
‡Behavioural Ecology and Self-organization, Centre for Ecological and Evolutionary Studies, University of Groningen, Groningen, The Netherlands

Keywords:

adult sex ratio;
mate choice;
mating system;
operational sex ratio;
parental care.

Abstract

Adult sex ratio (ASR) exhibits immense variation in nature, although neither the causes nor the implications of this variation are fully understood. According to theory, the ASR is expected to influence sex roles and breeding systems, as the rarer sex in the population has more potential partners to mate with than the more common sex. Changes in mate choice, mating systems and parental care suggest that the ASR does influence breeding behaviour, although there is a need for more tests, especially experimental ones. In the context of breeding system evolution, the focus is currently on operational sex ratios (OSRs). We argue that the ASR plays a role of similar importance and urge researchers to study the ASR and the OSR side by side. Finally, we plead for a dynamic view of breeding system evolution with feedbacks between mating, parenting, OSR and ASR on both ecological and evolutionary time scales.

> The great importance of the adult sex ratio has long been recognized by the student of human populations, but it has not received as much attention from the animal biologist as it deserves.
>
> (Mayr, 1939)

> Some researchers have suggested that the ASR is a major factor in sex role evolution, but their ideas have not been incorporated into mainstream theory.
>
> (Kokko & Jennions, 2008)

Introduction

Sex ratios and sex allocation are fundamental concepts in evolutionary biology (Hardy, 2002; West, 2009). The ratios of males to females at conception, at birth and during adult life (termed primary, secondary and adult sex ratio, respectively), have pervasive influences on ecology, behaviour and life histories. Primary sex ratio (PSR) plays a central role in sex ratio theory, as selection on PSR is negatively frequency dependent, and there are clear equilibrium predictions for a variety of scenarios, including differential costs in raising male and female offspring, differential effects of parental condition on the reproductive values of male and female offspring, and local mate competition (Trivers, 1985; West, 2009). However, PSR rarely translates directly into ASR, as various ecological, life history and demographic processes modulate the transition from PSR to ASR (see below). Consequently, the causes and implications of ASR variation may depend on numerous ecological and evolutionary processes.

Although many animals spend a substantial part of their life as adults, most research in evolutionary ecology of sex ratios has been directed to pre-adult sex ratios. This bias is striking for three reasons. Firstly, as the lack of direct frequency-dependent selection on the ASR means there is no guarantee that ASR biases remain insignificant, one would expect intense research to uncover the processes that create biased ASRs. Secondly, the ASR may affect mate choice, mating system and parental care (Mayr, 1939; Trivers, 1972; Breitwisch, 1989), and therefore, ASR appears to make a substantial, yet not fully understood, impact on

Correspondence: Tamás Székely, Department of Biology & Biochemistry, University of Bath, Bath BA2 7AY, UK.
Tel.: +44 1225 383676; fax: +44 1225 386779;
e-mail: T.Szekely@bath.ac.uk

breeding system evolution. Thirdly, the ASR in part *via* the number of females impacts on population growth, and therefore, has implications for population dynamics, risk of extinctions and biodiversity conservation (Bessa-Gomes *et al.*, 2004; Donald, 2007; Veran & Beissinger, 2009; Wedekind *et al.*, 2013). However, no recent review evaluates ASR variation across a broad range of organisms, and the implications of this variation for breeding systems and population demography – in contrast to numerous reviews on primary and secondary sex ratios (e.g. Charnov, 1982; Trivers, 1985; Hardy, 2002; West, 2009; Komdeur, 2012).

At first sight, one might imagine the ASR to be easier to determine than PSR because in many species sexing adults is easier than of newborn individuals. However, whereas establishing the ratio of male and female offspring in a litter or brood (secondary SR or offspring SR) may be a simple task facilitated by DNA-based sexing, doing the same for adults can be challenging in wild populations; as nonbreeding adults (e.g. floaters) often have nonconspicuous lifestyles and remain unnoticed, adult males and females may have different detectabilities due to sex difference in behaviour and ecology, and adults may form sex-specific aggregations during breeding and/or nonbreeding periods. Therefore, reliable ASR estimates often require capture–recapture estimates and demographic modelling (Veran & Beissinger 2009, Kosztolányi *et al.*, 2011).

We have three objectives in this article. First, we investigate the processes that may produce ASR bias, and highlight some of the striking examples of ASR variation in natural populations. The term 'adult' refers to an animal (male or female) that is physiologically capable of producing offspring. ASRs are often expressed as proportion of males in the adult population. We do not cover simultaneous hermaphrodites or sex-changing organisms (i.e. sequential hermaphrodites). Second, we discuss the implications of the ASR for breeding system evolution and argue that the ASR and operational sex ratio (OSR, ratio of sexually active males to females, see below) have a dynamic relationship. Understanding the OSR does not necessarily reveal much about the ASR, and *vice versa*. Thirdly, we propose three topics for further research. Future studies in these areas are likely to provide new insights into breeding systems and sex role evolution. Although we do not explore humans or plants in this article, we note that the ASR may also have relevance for human behaviour, demography and economic decisions (Trent & South, 2011; Griskevicius *et al.*, 2012; Székely & Székely, 2012; Schacht *et al.*, 2014), and for plant breeding systems (Taylor, 1999; Medrano *et al.*, 2005; Field *et al.*, 2013).

Causes of variation in adult sex ratios

Adult sex ratio emerges as the result of sex-specific processes affecting sex ratio at various life cycle stages including primary sex ratio, secondary sex ratio or sex ratio at independence (Fig. 1). Various factors can result in biased ASRs: a biased sex ratio at birth, sex-differential mortalities of young and adults, sex-differential maturation times, and sex-differential dispersal and migration patterns (Fig. 1, Wilson, 1975; Bessa-Gomes *et al.*, 2004; Veran & Beissinger, 2009). Differences in the maturation times of males and females are well known in various organisms (Daan *et al.*, 1996; Stamps & Krishnan, 1997; Donald, 2007), although their impact on the ASR is rarely explored (but see Hirst *et al.*, 2010). Sex differences in movement patterns are ubiquitous in the animal kingdom, and they can cause extreme ASR at the local level; at a metapopulation level, however, these local biases may balance out, as if an animal moves out from a population it has to move in another population assuming it remains alive.

In contrast to frequency-dependent selection operating on primary sex ratio, there are no similar predic-

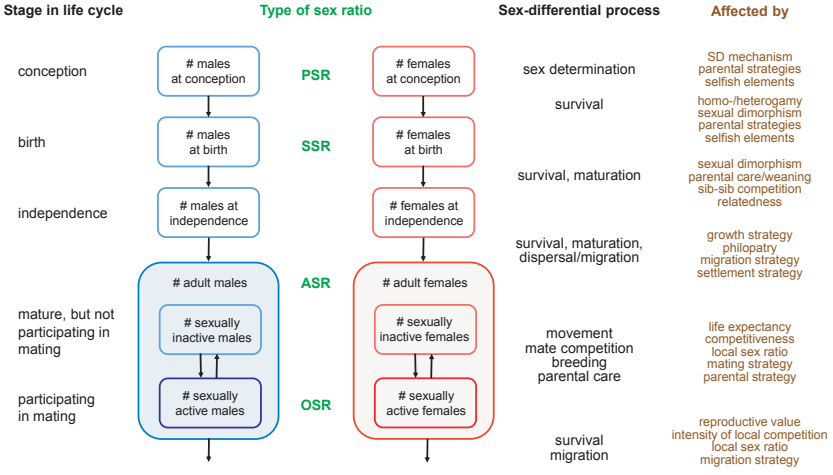

Fig. 1 A schematic representation of the sex-differential processes affecting sex ratio at various stages in a life cycle: primary sex ratio (PSR), secondary sex ratio (SSR), adult sex ratio (ASR) and operational sex ratio (OSR). A bias in ASR may reflect a bias in PSR, and SSR and/or sex differences in maturation, dispersal and survival. A bias in OSR may reflect a bias in ASR and/or sex differences in behaviours affecting participation in the 'mating market' such as sexual receptivity, parental care and post-care recovery. SD refers to sex determination.

tions for adult (or tertiary) sex ratios, as in sexually reproducing diploid organisms, the total reproductive value of all adult males equals the total reproductive value of all adult females irrespective of the sex ratio. As a consequence, sex ratio biases in adults are not directly selected against by a compensating adjustment of the PSR, as any increase in the abundance of, say, males is exactly compensated by a reduction in the average reproductive value of individual males. However, as discussed below, a bias in the ASR can initiate numerous ecological and evolutionary processes that indirectly feedback on this bias (Fig. 2). In the remainder of this section, we investigate potential causes of ASR variation.

Offspring sex ratios

Sex ratios are already biased early in life (i.e. at conception or at birth) in numerous organisms which can be adaptive, for instance if the cost (or benefit) of care differs for male and female offspring (e.g. in mammals, sons may drink more milk than daughters, sons may compete locally for the access to daughters, maternal condition may influence differentially the reproductive success of sons and daughters, Clutton-Brock, 1991; Trivers, 1985; West, 2009). Hatchling sex ratios are often biased in species with environmental sex determination, for instance hatchling sex ratios are temperature dependent in numerous fishes and reptiles (Pen *et al.*, 2010). Biased secondary sex ratios can be either enhanced (or diminished) by sex-differential juvenile mortality leading to biased sex ratio at maturation. In sexually dimorphic birds and mammals, sex-biased mortality often reflects the direction of sexual size dimorphism: male mortality is higher when males are the larger sex, and female mortality is higher when females are larger than males (Clutton-Brock, 1991; Kalmbach & Benito, 2007). These differences are attributed to the larger sex either being more sensitive to food shortages (Clutton-Brock, 1986; Kalmbach & Benito, 2007), or shifted away from its ecological optimum, if size dimorphism is induced by sexual selection (Andersson, 1994).

Biased juvenile mortality also occurs in sexually monomorphic species, although the cause of these biases is often obscure. In common eiders *Somateria mollissima,* the hatching sex ratio does not deviate from parity, but a male-biased sex ratio soon becomes established due to the higher mortality of female ducklings presumably caused by female-biased predation of chicks (Lehikoinen *et al.*, 2008). In Kentish plover *Charadrius alexandrinus,* hatchling mortality is female biased (for unknown reasons), and the sex difference in juvenile mortalities generates strongly male-biased ASR (Kosztolányi *et al.*, 2011).

Sex difference in the age of maturation

Maturation rates may differ between the sexes. Sex differences in the age of maturation may produce a biased ASR, as seems to be the case in fruit flies, fishes, salamanders and turtles (Lovich & Gibbons, 1990; Pitnick, 1993; Osmundson, 2006; Kusano & Inoue, 2011). In common voles *Microtus arvalis*, females mature earlier than males, and therefore, more females than males are

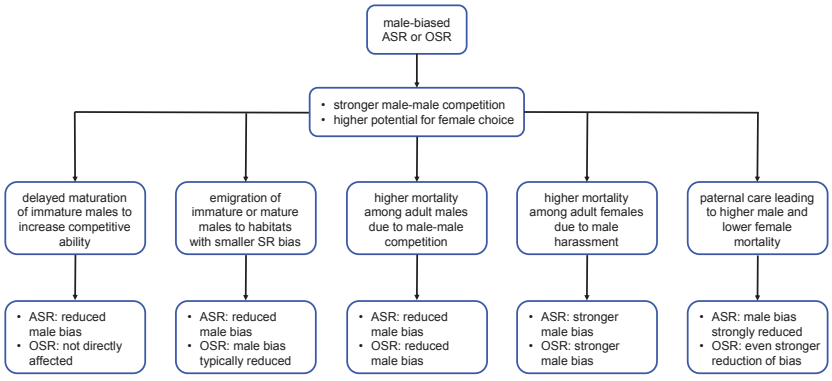

Fig. 2 Illustration of feedbacks on the adult and operational sex ratio. A bias in the adult sex ratio (ASR) may affect the intensity of male–male competition for resources, and a bias in the operational sex ratio (OSR) may affect the intensity of male–male competition for mates and the costs and benefits of female choosiness. Here, we only indicate five possible evolutionary and demographic implications that result from potential responses of males to a change in competition intensity or female choosiness. These can either reduce or enhance the original bias in the ASR and the OSR, and the effect size on both types of sex ratio can differ. Females may respond as well, both in their choosiness and in their reaction to the males' responses indicated in the figure. For example, a shift to paternal care (boxes to the right) could induce females to spend less time on parenting and more time on mating; this would further reduce or even reverse the original OSR bias. For simplicity, female responses are left out from the figure. Footnote 1 (lower box to the left): provided that only those males delay their maturation that are not sufficiently competitive and would not participate in matings anyhow.

recruited to the adult population in early summer (Bryja *et al.*, 2005).

Maturation, in turn, can be influenced by adult mortalities and the ASR. For example, if old and/or large animals are selectively eliminated from the population (for instance, by trophy hunters or a predator specialized on taking large preys), males and/or females may shift towards maturing fast and reproducing at an early age (Roff, 2002). In humans, male-biased ASR is associated with early puberty and an increased likelihood that a woman marries before the age of 25 and engages in more premarital and extramarital sexual relationships (Andersson, 1994; Trent & South, 2011).

Sex difference in adult lifestyles

Adult males and females often have different body sizes and body shapes, behaviour, ornaments and armaments (Arnqvist & Rowe, 2005; Fairbairn *et al.*, 2007; Székely *et al.*, 2010), and these sex differences can precipitate into differences in energy consumption, foraging ecology and mortalities – ultimately influencing the ASR. Consistently, in many organisms, sex ratio bias only emerges during (or close to) adulthood. For instance, ASR bias in birds and reptiles emerges from even juvenile sex ratios due to sex-biased mortality after reaching adulthood (Donald, 2007). Furthermore, the sex ratio in mosquitofish *Gambusia affinis* shifts from an even PSR to a female-biased ASR, as adult males are less resistant to extreme temperatures than females (Krumholz, 1948). Temperature-dependent mortality appears to induce a large shift in fish ASR (Wedekind *et al.*, 2013); thus, future climatic changes may potentially affect the ASR of fish populations.

Adult males and females often represent different ecotypes with different lifestyles. For example, females are often cryptic, whereas males are more exposed to predators, especially when they are seeking mates (Pettersson *et al.*, 2004; Brouwer, 2007). Conversely, pregnant, incubating or nursing females are more vulnerable because their fleeing capabilities are reduced, and they need to spend more time feeding to cope with increased energy demands (Clutton-Brock, 1991). A strong diurnal pattern in incubation behaviour by males and females may create sex-biased mortalities in Seychelles warblers *Acrocephalus sechellensis,* as common mynahs *Acridotheres tristis* predate during the day when females are incubating (Brouwer, 2007; van der Woude unpublished data). Sex-biased predation may also result if males and females have different nutritional value (e.g. different fat content) causing predators to preferentially hunt the sex with the highest value, or if males force females into habitats that are more exposed to predators (Darden & Croft, 2008).

Given these contrasting predictions, is there a systematic pattern in data with predation bias on males or females? Differential predation is a common cause of biased ASR in fishes, frogs, birds and mammals (Magnhagen, 1991; Berger & Gompper, 1999; Sargeant *et al.*, 2004; Christe *et al.*, 2006; Post & Gotmark, 2006). Male-biased predation is 2.3 times more common than female-biased predation in 81 predator–prey species pairs, suggesting that predators often have male-biased prey preference, or they encounter males more often than females (Boukal *et al.*, 2008). Male-biased predation is not only more common, but also reaches more extreme values (Boukal *et al.*, 2008).

Sex-biased predation rates may vary between predators. Although males are predated more often than females in 23 of 31 ungulate species (Berger & Gompper, 1999), in Thomson gazelles *Gazella thomsonii,* the odds of getting killed by wild dogs *Lycaon pictus* were six times higher for males than for females, whereas the odds of getting killed by cheetahs *Acinonyx jubatus* were higher for female gazelles (Berger & Gompper, 1999). The same predator may induce different sex biases in predation rates in different prey species: when attacked by African lions *Panthera leo,* the likelihood of being killed is 7.3 times higher for male than for female African buffalos *Syncerus caffer*, whereas in reedbuck *Redunca redunca,* only females are killed (Schaller, 1972).

Parasites and diseases may also create sex-biased ASR. In mammals, infections by arthropods, helminths and unicellular parasites are often male-biased, suggesting that males invest less into their immune system (Moore & Wilson, 2002), and this correlates with male-biased mortalities (and female-biased ASRs). Differential morbidity may also emerge if one sex is more sensitive to a particular type of parasite (or disease) than the other.

The effect of parasites on the sex ratio of their host may interact with the ecology of the host. For example, the influence of microsporidian parasite *Edhazardia aedis* was studied as a function of larval food availability to its host, the mosquito *Aedes aegypti* (Agnew *et al.*, 1999). The number of infected mosquitoes dying before adulthood increased as larval food availability decreased. However, proportionately more female mosquitoes died as food availability decreased, so that the adult mosquito populations became increasingly male-biased (Agnew *et al.*, 1999).

Anthropogenic sources of mortality can also be sex dependent, even when there is no explicit aim to influence mortality, for example by hunting, in a sex-specific way. For instance, size-selective fishing affects sex ratios in salmon (Kendall & Quinn, 2013), and female-biased mortality is caused by cutting the hay during incubation in a meadow bird, the whinchat *Saxicola rubetra*, in which only females incubate the eggs (Grubler *et al.*, 2008).

Sex determination, sex distorters and adult sex ratios

Sex determination systems may also influence the ASR. First, one would expect that in organisms with

chromosomal sex determination, the heterogametic sex (males in mammals; females in birds and butterflies) is more vulnerable as harmful mutations cannot be 'masked' in the homogametic sex. In line with this, males tend to have a higher mortality in mammals, whereas the opposite is reported in birds and butterflies (Berger & Gompper, 1999; Liker & Székely, 2005; Donald, 2007). These patterns are in line with Haldane's rule which states that hybridization leads to reduced vitality and fertility, and increased early mortality especially in the heterogametic sex (Schilthuizen *et al.*, 2011).

Second, besides having a direct effect on sex-differential mortality, the mechanism of sex determination has a more subtle effect on selection differentials. The dynamics of genetic variation on sex chromosomes (where genes related to sex differences tend to accumulate) is different between the genes occurring in only one sex (the Y in mammals, the W in birds and butterflies) and the genes that occur in both sexes. As a consequence, theory predicts marked differences in sex roles that are associated with sex chromosomes (Haig, 2006). For example, the different sex-determining mechanisms in birds and mammals may cause a sex difference in philopatry (mammals: typically male-biased dispersal; birds: female-biased dispersal, Haig, 2006), male–male competition (mammals: strong; birds: relatively weaker) and female choice (mammals: relatively weaker; birds: stronger). It is obvious that philopatry, male–male competition and female choice can potentially influence the ASR (Fig. 1).

Third, sex determination can have an effect on the sex ratio at conception (primary sex ratio) and, hence, indirectly affect the ASR. Sex-specific lethality or sex change can be induced by 'selfish' genetic elements (often transmitted with the cytoplasm), or microorganisms such as *Wolbachia*. Microbes and cytoplasmically inherited symbionts are common in arthropods and are well known to bias sex ratios of their hosts early in life (Burt & Trivers, 2008), and these may precipitate into biased ASRs. Some cytoplasmatic genetic elements (including microorganisms like *Wolbachia*) are vertically transmitted through the female line (as sperm does not contain cytoplasm); accordingly, males are a dead-end road for such genetic elements, and they are only interested in female survival and reproduction.

As a consequence, these elements come up with a multitude of tricks to shift the sex ratio in favour of females that include male-killing, feminizing males and making females parthenogenetic. They sometime produce spectacularly female-biased ASRs, such as 100 female to 1 male (e.g. in isopods, fruit flies, butterflies; Engelstädter & Hurst, 2009; Price & Wedell, 2008). Experimental support comes from *Eurema hecabe* butterflies that have female-biased ASR: experimentally treated butterflies with antibiotic reverted to 1 : 1 ASR after treatment (Narita *et al.*, 2007).

Spatial and temporal variation in adult sex ratios

The different sources of biases create strikingly diverse ASRs between species and populations. Some patterns appear to exist, although it would be premature to make categorical statements about many animal taxa. For example, copepods and mammals tend to have female-biased ASR, whereas male-biased ASR occurs in Schistosoma parasites and birds (Fig. 3; Beltran *et al.*, 2009; Donald, 2007). Some of the most extreme bias occurs among marsupials (Didelphidae and Dasyuridae): in the dusky antechinus *Antechinus swainsonii* and in eight other marsupials, males abruptly die after the mating season, there are times when no adult males are alive and the entire population is made up of pregnant females (Cockburn *et al.*, 1986).

Adult sex ratio may vary in time, and in open populations, some of this variation is due to dispersal (emigration and immigration), or demographic stochasticity that can cause considerable spatial and temporal fluctuations in the ASR in small populations increasing the risk of extinction (Dale, 2001; Bessa-Gomes *et al.*, 2004). Nevertheless, ASR fluctuates even in closed populations due to biases in the primary and/or secondary

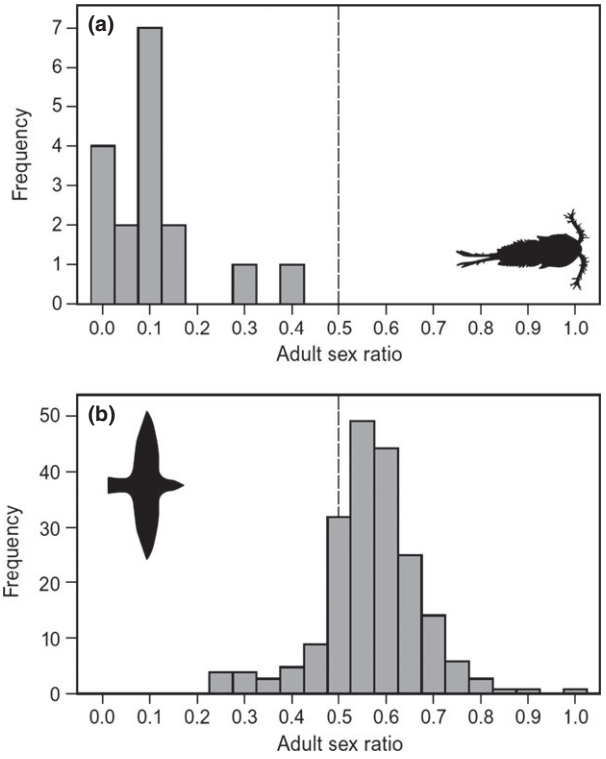

Fig. 3 Adult sex ratios in copepods (a, Gusmao & McKinnon, 2009) and birds (b, Donald, 2007). Frequency refers to the number of species, whereas adult sex ratio is the proportion of males in the adult population.

sex ratios, sex-differential mortalities or maturation rates (Fig. 4, Donald, 2007; Hirst *et al.*, 2010). ASR varies over time, for instance, in the jumping spider *Phidippus clarus:* the males emerge before females so that the ASR is male-biased initially in the breeding season (protandry) shifting towards female bias after the females start emerging (Hoefler, 2007). In migratory birds, the more common sex (often males) experiences stronger competition for mates so is predicted to arrive earlier (Kokko *et al.*, 2006).

Adult sex ratio may also vary between different locations, for instance Trinidad guppy *Poecilia reticulata* populations in some streams exhibit significantly male-biased ASR, whereas others have unbiased or female-biased ASR (Fig. 5, Pettersson *et al.*, 2004). As the sex ratio of juveniles is unbiased in all of these populations, the biased ASR appears to result from sex-differential mortality, which in turn reflects spatial differences in natural and sexual selection (Pettersson *et al.*, 2004; McKellar *et al.*, 2009). Male guppies appear to be more sensitive to high temperatures than females; thus, temperature differences between sites are expected to impact upon the ASR (Pettersson *et al.*, 2004). In addition, with males being more colourful and active than females, the males are predated more often than the females by one predator (killifish *Rivulus hartii*) but not by another (freshwater prawn *Macrobrachium crenulatum*; McKellar & Hendry, 2011). Therefore, variation in predator densities between streams may also contribute to ASR variation (McKellar & Hendry, 2011).

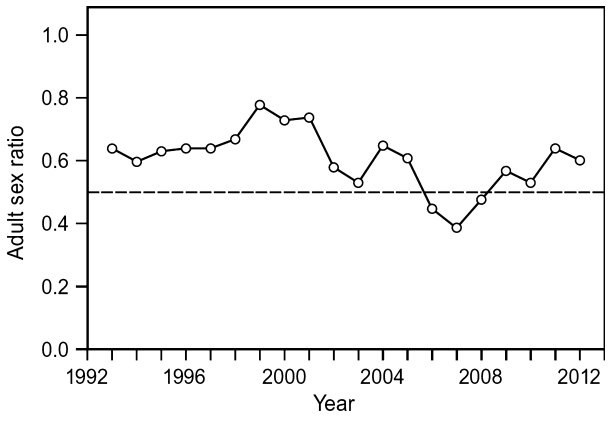

Fig. 4 Adult sex ratio (proportion of adult males) of song sparrows *Melospiza melodia* on Mandarte Island over a 20-year period (Reid, Keller and Arcese unpubl. data).

However, the aforementioned studies have two major limitations. First, no study has tested comprehensively whether ASR bias is due to biased offspring sex ratio, and/or sex difference in maturation and/or survival of juveniles and adults, and thus integrate over the major processes that produce the ASR. Second, most studies that investigated components of ASR variation were nonexperimental. As the ecology, physiology and behaviour of organisms tend to covary, it is difficult to disentangle which aspect of animal's life is causally related to sex-biased mortalities and thus to ASR biases. As demonstrated by Maly (1970), causal analysis can sometimes be performed using controlled and replicated laboratory experiments. He investigated sex-specific intake rates of three different predators feeding on two species of *Diaptomus* copepods. Tadpoles *Ambystoma tigrinum* ate more female than male copepods, guppies ate more males than females, whereas *Hydra cauliculata* ate equal numbers of male and female copepods. Male copepods are more active than females, and this activity difference coupled with the different hunting style of predators produced the bias in prey composition: tadpoles stalk their prey and they capture primarily slowly moving prey, guppies hunt the faster moving prey, whereas *Hydra* feeding is passive and they eat prey that swim into their tentacles. Remarkably, the copepod ASRs in natural ponds were consistent with the results of the laboratory experiments (Maly, 1970).

Implications of adult sex ratios for mate choice, pair bonds and parental care

Theory suggests that the ASR should influence mate acquisition, mating systems and parental care (McNamara

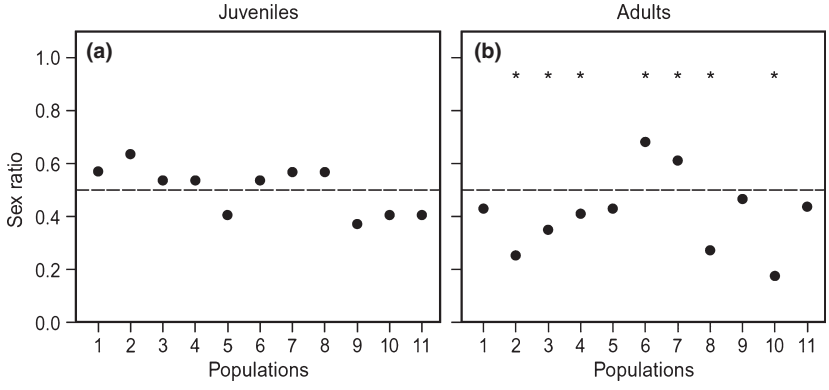

Fig. 5 Juvenile (a) and adult sex ratios (b) in 11 guppy populations in Trinidad (Pettersson *et al.*, 2004). Star indicates sex ratios significantly different from 0.5 and expressed as proportion of males.

et al., 2000; Székely *et al.*, 2000; Kokko & Jennions, 2008). Consistently with theoretical expectations, observational, experimental and comparative studies suggest that the ASR influences (or correlates with) various aspects of breeding behaviour, as the rarer sex in the population has more potential partners to mate with than the more common sex.

Mate acquisition

Adult sex ratio influences pairing behaviour, male–male, female–female and male–female interactions (Alonzo & Sheldon, 2010). Males may move away from male-biased patches (Croft *et al.*, 2003; Steifetten & Dale, 2012), or if they stay, they intensify courtship and/or competition for mates, for instance in gobies Gobiidae and pipefishes Syngnathidae (Kvarnemo *et al.*, 1995; Forsgren *et al.*, 2004; Silva *et al.*, 2010).

When the ASR is heavily biased, the sex in excess may engage in homosexual pairings or seek mates from a congeneric species. Consistently, female-biased ASR appears to induce female–female pairings in seabirds (Tershy & Croll, 2000): Laysan albatross *Phoebastria immutabilis* has a female-biased ASR, and 31% of pairs were female–female pairs (Young *et al.*, 2008). Coinciding with strongly female-biased ASR in western gulls *Larus occidentalis*, female–female pairs constituted at least 10% of the breeding population (Hunt *et al.*, 1980). Homosexual pairing has also been observed in captive or domestic birds held in groups with highly skewed sex ratios (Collias & Jahn, 1959; Dilger, 1960; Sauer, 1972). Furthermore, the lack of suitable mating partners has been proposed to lead to hybridisation between different tern species (Whittam, 1998).

Adult sex ratio may influence developmental pathways of juveniles to prepare for mate acquisition as adults. In dung beetles *Onthophagus spp.*, male-biased ASR appears to trigger the development of horns that are used as weapons, whereas in populations with female-biased ASR, males tend to be hornless (Pomfret & Knell, 2008).

Mating system and paternity

Male-biased ASR was associated with higher frequency of polyandry in dunnock *Prunella modularis* and lesser spotted woodpecker *Picoides minor* (Davies, 1992; Rossmanith *et al.*, 2006), whereas in song sparrows *Melospiza melodia,* males were monogamous in years when there was an excess of males, but tended towards polygyny when the ASR became female biased (Smith *et al.*, 1982). Comparative studies support the findings of these single-species studies, at least in birds: polygamy by males is significantly more common at female-biased ASR than at male-biased ASR, whereas polygamy by females is more common at male-biased ASR (Liker *et al.*, 2013, 2014). Thus, the rarer sex can exploit the favourable mating opportunities provided by biased ASR, and desert his/her mate and renest with a new mate (Pilastro *et al.*, 2001).

Extra-pair paternity occurs in a wide range of organisms, although we are not aware of any theoretical model that would link ASR to mate guarding and paternity. Male-biased ASR may be associated with multiple paternities in two ways. On the one hand, multiple paternity may increase with male-biased ASR as there are more males per female (e.g. in *Rana dalmatina* frogs, Lode *et al.*, 2004). Fruit fly *Drosophila melanogaster* males experimentally kept at male-biased ASR depleted their ejaculates faster than males kept at female-biased ASR (Linklater *et al.*, 2007). Therefore, male reproductive traits appear to have evolved in response to the level of sperm competition, and associated with the rate of ejaculate depletion and the degree of ASR. On the other hand, males may respond to male-biased ASR by intensifying mate-guarding behaviour that reduces multiple paternities (Harts & Kokko, 2013). This appears to be the case in frogs, spiders and crustaceans (Fromhage *et al.*, 2005; Karlsson *et al.*, 2010; Takeshita & Henmi, 2010).

Intuitively, ASR is expected to influence pair bonds and divorces, although we are not aware of a specific theoretical model. Unbalanced sex ratios may destabilize pair bonds and induce divorces, although it is not clear whether these effects work through influencing mortality rates (and thus impacting mate availability), or via behaviour for instance one sex harasses (or entice) mated members of the others sex that lead up breaking up existing pair bonds (Liker *et al.*, 2014). Experimentally altered ASR has influenced mating rates (or divorce) in lobsters, fishes and mice (Delong, 1978; Keenleyside, 1983; Balshine-Earn & Earn, 1998; Debuse *et al.*, 1999; Beltran *et al.*, 2009; Karlsson *et al.*, 2010; Silva *et al.*, 2010). An elegant manipulation of the ASR in the endoparasitic trematode *Schistosoma mansoni* showed that male-biased ASR induced more divorce than even female-biased ASR (Fig. 6).

Male-biased ASR was experimentally created in domestic pigeons *Columbia livia* during half of the breeding season, whereas the ASR was reverted to even for the second half of season (Marchesan, 2002). During the male-biased period, clutch failure rate increased, and there were more within-pair copulations and a higher proportion of pairs divorcing presumably due to intense male–male harassment. Although the experiment was not fully controlled as male-biased and control ASR were achieved in different parts of the breeding season, the results are consistent with the explanation that surplus of males are detrimental to the breeding population.

Sexual conflict and male harassment

Adult sex ratio has often been used to induce variation in sexual conflict (Holland & Rice, 1999; Wigby &

Chapman, 2004; Arnqvist & Rowe, 2005; Fitze & Le Galliard, 2008). Consistently with expectations, female mating rate increased with male-biased ASR in fruit flies *Drosophila melanogaster* (Wigby & Chapman, 2004). Furthermore, the duration of mate-guarding, mating duration and mating rate tended to have higher values in male-biased, compared to female-biased adult sex ratios in water striders *Gerris spp.* (Arnqvist & Rowe, 2005).

Male-biased ASR (i.e. male skew) may lead to high male aggression and reduced female survival (Hailey & Willemsen, 2000; Le Galliard *et al.*, 2005). The excess of males in common lizard *Lacerta vivipara* induces aggression towards females, whose survival and fecundity drop. The ensuing prediction is that male skew should be amplified and total population size should decline. Numerical projections show that this amplifying effect strongly enhances the risk of population extinction (Bessa-Gomes *et al.*, 2004).

Parental care

Theoretical models predict that male-biased ASR should induce more care by the male, whereas female-biased ASR should induce more care by the female (McNamara *et al.*, 2000; Kokko & Jennions, 2008). However, there is mixed support for these predictions (Keenleyside, 1983; Breitwisch, 1989; Balshine-Earn & Earn, 1998). Experimental manipulation of the ASR in cichlid fish *Herotilapia multispinosa* found that brood-guarding males deserted their mates and broods more frequently in the presence of a surplus of females (Keenleyside, 1983). However, female parents did not desert their mates, regardless of the sex ratio.

In birds, the evidence for ASR-driven parental care is also mixed (Breitwisch, 1989). In captive zebra finches, *Taeniopygia guttata* male-biased ASR induced more parental care from males compared to female-biased ASR, but there was no difference in female parental behaviour (Burley & Calkins, 1999). In shorebirds, however, parental behaviour of both males and females was related to the ASR: at male-biased ASR, male care increased whereas female care decreased, whereas at female-biased ASR, the opposite patterns were observed (Liker *et al.*, 2013).

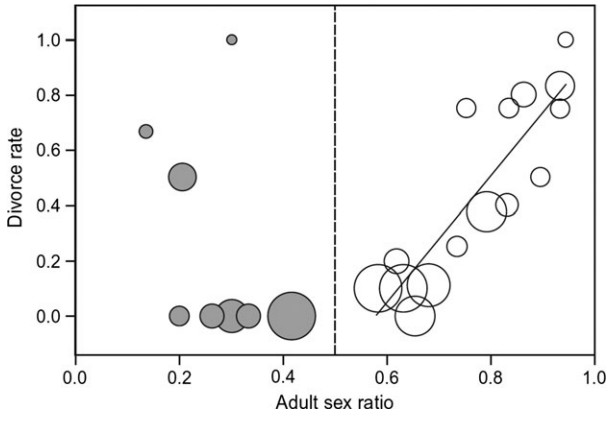

Fig. 6 Influence of the adult sex ratio (proportion of adult males) on divorce rate in an endoparasitic trematode *Schistosoma mansoni*. Experimental alteration of adult sex ratio (proportion of adult males) towards male bias (open circles, but not towards female-bias, shaded circles) increases divorce rates (Beltran *et al.*, 2009).

Strengths and weaknesses of ASR studies for breeding systems

Two major conclusions emerge from these studies. First, the responses to male-biased and female-biased ASR need not be symmetric. For instance, experimentally altering the ASR towards males increased divorce rate in trematode parasites, whereas female-biased ASRs induced no change in divorce rates (Beltran *et al.*, 2009). The reason for the different responses to male-biased and female-biased ASR appears to be female behaviour: females initiate the divorce, and they only seek divorce when the ASR is male-biased so that they have more options to choose high-quality mates (Beltran *et al.*, 2009).

Second, it is often difficult to pin down whether a particular relationship between the ASR, mating and parenting is due to changes in male behaviour, female behaviour or the interaction of both sexes. Mate choice, pair bonds and parenting emerge via social interactions (see below), and the social strategies of individuals are not always directly visible. For example, unmated individuals (e.g. floaters) should not be ignored when studying mate choice or parenting decisions, as the presence of such individuals may strongly affect the mating (or parenting) decisions of the breeding part of the population, even if they neither mate nor care for the young (Webb *et al.*, 2002).

The majority of the aforementioned studies, however, were nonexperimental, and it is therefore difficult to disentangle cause and effect. For instance, a correlation between the ASR and mating system may also emerge if food distribution varies between years, and the change in mating system is driven by the spatial distribution of food resources that coincides with ASR shift (Davies & Lundberg, 1984; Prohl, 2002). Studies that did manipulate ASR directly and investigated the animals' responses to altered ASR, however, were often carried out in the laboratory so that it is not known how realistic the animals' responses were to the experimentally altered sex ratios. In addition, in laboratory experiments, the animals' options are constrained, for instance, as a response to reduced mating opportunities they may not be able to move to a different habitat as they would do in wild populations.

Operational sex ratio and adult sex ratio

The operational sex ratio (ratio of sexually active males to females, OSR, Kvarnemo & Ahnesjö, 1996; Shuster &

Wade, 2003) has played a central role in the context of sexual selection, mating systems and breeding system research (note that in their seminal paper, Emlen & Oring, 1977 defined OSR as the ratio of fertilizable females to sexually active males). The OSR, however, has shortcomings: it is often not trivial to judge whether an individual is sexually active or not, for instance if sexual activity does not have a clear visual or olfactory cue, like sexual swellings in female primates. Many males are able to fertilize females even if they are in a pair bond or caring for young. Sometimes, it is tricky to work out who actually counts, for instance in leks there are only a few males the females are interested in mating, whereas there are many males off the lek that are excluded from mating (Bro-Jorgensen, 2007). Therefore, lek-based OSR estimates may give a very different OSR from the population-level OSR.

There is a general tendency to equate the ASR and the OSR (Kokko & Jennions, 2008; Weir *et al.*, 2011). A possible reason is that in most experimental studies, both ratios are manipulated simultaneously using the starting condition where all adults contribute to the OSR (Kokko pers comm). For example, X mature males and Y mature females are placed in an enclosure and then the reproductive variable of interest is measured. Variation among enclosures is then attributed to variation in X: Y which is almost always labelled as the OSR rather than the ASR (Alonso-Pimentel & Papaj, 1999; Jirotkul, 1999; Klemme *et al.*, 2007; but see Fitze & Le Galliard, 2008). This may not be correct because the sexual activity of males and females (and thus OSR) may change during the course of the experiment as some of them pair up, look after the young or lose interest in mating.

The ASR and the OSR may substantially differ in wild populations (Fig. 1). First, the sexually available periods of males and females are rarely identical, as males and females may need different times to prepare physiologically for breeding, their receptive periods may have different duration, males and females may contribute differentially to parental care and have different post-care recovery periods. Therefore, cases where the OSR and the ASR are identical appear to be the exception, rather than the rule. For example, the OSR is expected to be male biased both in mammals and birds, although in mammals, the male-biased OSR may emerge from female-biased ASR due to females providing offspring care for substantially longer than males, whereas in birds, the male-biased OSR may emerge from male-biased ASR *via* monogamous social pair bonds and biparental offspring care.

Second, *time in*-s and *time out*-s (i.e. time periods when an individual is sexually available or unavailable for mating, respectively) can be phenotypically plastic as a response to OSR, as animals may spend more time sexually active when chances of breeding are high (i.e. increased *time in*), whereas high mating opportunity may entice some adults to reduce parental caring periods and seek a new mate (i.e. reduced *time out*, Székely *et al.*, 2000; Parra *et al.*, 2014). Therefore, the correlation between the OSR and the ASR can be weak: longer *time in* (or shorter *time out*) may change the OSR, whereas the ASR remains constant.

As we argued above, ASR is primarily a demographic property of populations that emerges *via* sex differences in mortality, maturation rates and movement patterns (Bessa-Gomes *et al.*, 2004; Le Galliard *et al.*, 2005; Veran & Beissinger, 2009; Kosztolányi *et al.*, 2011). On top of this, the OSR emerges *via* individuals' decisions whether to join the breeding population, and how long to opt out from breeding during (and after) periods of parental care (Clutton-Brock & Parker, 1992; Kokko & Jennions, 2008). As the OSR is partly due to short-term changes between mating decisions, parental care and post-care recovery, the OSR by definition 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 systems and parental care, rather than an external factor that 'explains' mating systems (Fig. 2; Székely *et al.*, 2000; Donald, 2007). To a certain extent, this may also apply to the ASR (see below), as sex differences in mortality, maturation and movement may also reflect reproductive decisions, such as fighting for territories, delaying maturation to become more competitive and moving to locations with a lower degree of reproductive competition, although given the ASR's dependence on demographic processes, the effect appears to be weaker.

The dynamics of adult sex ratios, mating system and parental care

The demographic and behavioural processes that generate the ASR and the OSR are only partly independent, and they both interact with breeding behaviours (Fig. 1). So far, we emphasized the feedbacks between the OSR, mating behaviours and parental care. Here, we focus on feedbacks between the ASR and mortality implications of breeding behaviours (Kokko & Jennions, 2008; Jennions & Kokko, 2010).

The aforementioned empirical studies should be interpreted with bearing in mind that responses to ASR may involve plastic behavioural responses and/or evolutionary responses manifested over phylogenetic time scales. Accordingly, it might be helpful to recognize two kinds of feedbacks: one on the ecological time scale directly affecting contemporary populations, and the other on an evolutionary time scale (Fig. 2, Jennions & Kokko, 2010; Klug *et al.*, 2012). On an ecological time scale, the movements of animals from and to particular locations can alter the local ASR. As one cause of animal's movements is seeking a mate or a suitable breeding territory, the breeding system in one location may

impact upon the sex-specific movement decisions and thus on the ASR. For instance, if in a polygynous species, the males are territorial and floating males are expelled from the local population, the resulting female-biased ASR is in part a consequence of the breeding system.

Feedbacks on an evolutionary time scale can be positive or negative (Lehtonen & Kokko, 2012; Liker *et al.*, 2013). On the one hand, biased ASR may increase the mortality of the more common sex and thus ASR may be self-correcting (Fisher, 1930). For instance, if the ASR is heavily male-biased, this may intensify mate competition and as such, increase male mortality. This process could counterbalance the biased ASR producing a more even ASR. Following Fisher's logic, Trivers (1972) noted that sex-specific mortality patterns tend to coevolve with sex-specific patterns of parental investment. For example, the male-biased adult mortalities and female-biased ASRs in mammals are often credited to intense male–male competition (Clutton-Brock, 1991; Donald, 2007).

On the other hand, sexual selection, parenting and ASR may amplify each other via a positive feedback (Jennions & Kokko, 2010; Lehtonen & Kokko, 2012). Lack (1968) used a bird example to illustrate this logic in the context of sexual selection and enhanced male mortality: 'Hence, once polygynous mating system has evolved, the unusually strong competition for mates will lead to the males evolving brilliant plumage, which will increase their mortality from predation, which will make it disadvantageous for them to breed when one year old, so there will be a surplus of females, which will be forced to be polygynous, which will reinforce these trends.' Thus, populations may be locked into a heavily biased ASR. Whether the feedbacks are negative or positive, it may depend on the mortality costs of different activities such as the competition for mates and parenting (Fig. 2).

Conclusions and future directions

Adult sex ratio is a fundamental, yet somehow underappreciated, concept in evolutionary biology. Although substantial progress has been made since Mayr (1939), his main message still holds: evolutionary ecologists should put more effort into estimating the ASR, understanding the causes of ASR variation, and exploring the implications of ASR variation for breeding system evolution, sex roles and population dynamics.

Our review highlights three issues. First, researchers should clearly separate ASR and OSR, and be aware that they may contain different (and often complementary) information (Fig. 1). The OSR is a useful term, although it does not replace ASR, as the OSR itself is generated by the mating and parental decisions of animals themselves (Székely *et al.*, 2000; Kokko & Jennions, 2008; Alonzo & Sheldon, 2010). Biased OSR may emerge from unbiased ASR, and vice versa. As the ASR and the OSR contain complementary information, separating the effects of the ASR from the OSR would represent an important advance in studies of breeding system evolution.

Second, researchers should be aware of the dynamic nature of relationships with reciprocal causality and a multitude of feedbacks (Fig. 2). The ASR and the OSR have effects on sex roles and breeding systems, although sex roles and breeding systems, in turn, may influence individual decisions in a sex-specific manner which will affect the ASR and/or the OSR. Therefore, we plead for a dynamic view of breeding system evolution, with feedbacks on both ecological and evolutionary time scales.

Third, experimental studies are required to disentangle the thicket of cause and effect relationships. Experiments in laboratory, seminatural and wild environments can provide novel insights into the complex relationships between populations and individuals that may emerge via sex ratios, breeding behaviour and various selection processes operating on juveniles and adults. Studies are needed to manipulate the ASR and investigate its impact on mate choice, pair bonds and parental care. We hope that in 10 years' time, Mayr's quote will be reversed, as the importance of adult sex ratio will have received the much deserved attention from evolutionary biologists.

Acknowledgments

We acknowledge the comments of Hanna Kokko, Peter Kappeler, Michael Jennions, András Liker, Ido Pen, Steve Ramm and two anonymous reviewers on previous versions of the manuscript. TSz was funded by a Visiting Scholarship of the Erasmus Mundus Programme MEME at the University of Groningen, a Mercator Visiting Professorship at Bielefeld University and a Humboldt Award at the University of Göttingen. This research was supported by a TOP grant (854.11.003) from the Netherlands Organization for Scientific Research to JK and FJW.

References

Agnew, P., Bedhomme, S., Haussy, C. & Michalakis, Y. 1999. Age and size at maturity of the mosquito *Culex pipiens* infected by the microsporidian parasite *Vavraia culicis*. *Proc. R. Soc. B* **266**: 947–952.

Alonso-Pimentel, H. & Papaj, D.R. 1999. Resource presence and operational sex ratio as determinants of copulation duration in the fly *Rhagoletis juglandis*. *Anim. Behav.* **57**: 1063–1069.

Alonzo, S.H. & Sheldon, B.C. 2010. Population density, social behaviour and sex allocation. In: *Social Behaviour: Genes, Ecology and Evolution* (T. Székely, A. Moore & J. Komdeur, eds), pp. 474–488. Cambridge University Press, Cambridge.

Andersson, M. 1994. *Sexual Selection*. Princeton University Press, Princeton, NJ.

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

Balshine-Earn, S. & Earn, D.J.D. 1998. On the evolutionary pathway of parental care in cichlid fishes. *Proc. R. Soc. Lond. B* **265**: 2217–2222.

Beltran, S., Cézilly, F. & Boissier, J. 2009. Adult sex ratio affects divorce rate in the monogamous endoparasite *Schistosoma mansoni*. *Behav. Ecol. Sociobiol.* **63**: 1363–1368.

Berger, J. & Gompper, M.E. 1999. Sex ratios in extant ungulates: products of contemporary predation or past life histories? *J. Mammal.* **80**: 1084–1113.

Bessa-Gomes, C., Legendre, S. & Clobert, J. 2004. Allee effects, mating systems and the extinction risk in populations with two sexes. *Ecol. Lett.* **7**: 802–812.

Boukal, D.S., Berec, L. & Krivan, V. 2008. Does sex-selective predation stabilize or destabilize predator-prey dynamics? *PLoS ONE* **3**: e2687.

Breitwisch, R. 1989. Mortality patterns, sex ratios, and parental investment in monogamous birds. *Curr. Orn.* **6**: 1–50.

Bro-Jorgensen, J. 2007. Reversed sexual conflict in a promiscuous antelope. *Curr. Biol.* **17**: 2157–2161.

Brouwer, L. 2007. Cooperative breeding and density regulation in small island populations of the Seychelles warbler. Unpubl. PhD thesis, Groningen University, Netherland.

Bryja, J., Nesvadbova, J., Heroldova, M., Janova, E., Losik, J., Trebaticka, L. *et al.* 2005. Common vole (*Microtus arvalis*) population sex ratio: biases and process variation. *Can. J. Zool.* **83**: 1391–1399.

Burley, N.T. & Calkins, J.D. 1999. Sex ratios and sexual selection in socially monogamous zebra finches. *Behav. Ecol.* **10**: 626–635.

Burt, A. & Trivers, R. 2008. *Genes in Conflict*. Harvard University Press, Cambridge, MA.

Charnov, E.L. 1982. *Sex Allocation*. Princeton Monographs in Population Biology, Princeton, NJ.

Christe, P., Keller, L. & Roulin, A. 2006. The predation cost of being a male: implications for sex-specific rates of ageing. *Oikos* **114**: 381–394.

Clutton-Brock, T.H. 1986. Sex-ratio variation in birds. *Ibis* **128**: 317–329.

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

Clutton-Brock, T.H. & Parker, G.A. 1992. Potential reproductive rates and the operation of sexual selection. *Q. Rev. Biol.* **67**: 437–456.

Cockburn, A., Scott, M. & Dickman, C. 1986. Sex ratio and intrasexual kin competition in mammals. *Oecologia* **66**: 427–429.

Collias, N.E. & Jahn, L.R. 1959. Social behavior and breeding success in Canada geese (*Branta canadensis*) confirmed under semi-natural conditions. *Auk* **76**: 478–509.

Croft, D.P., Albanese, B., Arrowsmith, B.J., Botham, M., Webster, M. & Krause, J. 2003. Sex-biased movement in the guppy (*Poecilia reticulata*). *Oecologia* **137**: 62–68.

Daan, S., Dijkstra, C. & Weissing, F.J. 1996. An evolutionary explanation for seasonal trends in avian sex ratios. *Behav. Ecol.* **7**: 426–430.

Dale, S. 2001. Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. *Oikos* **92**: 344–356.

Darden, S.K. & Croft, D.P. 2008. Male harassment drives females to alter habitat use and leads to segregation of the sexes. *Biol. Lett.* **4**: 449–451.

Davies, N.B. 1992. *Dunnock Behaviour and Social Evolution*. Oxford University Press, Oxford.

Davies, N.B. & Lundberg, A. 1984. Food distribution and a variable mating system in the dunnock (*Prunella modularis*). *J. Anim. Ecol.* **53**: 895–912.

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

Delong, K.T. 1978. The effect of the manipulation of social structure on reproduction in house mice. *Ecology* **59**: 922–933.

Dilger, W.C. 1960. The comparative ethology of the African parrot genus *Agapornis*. *Z. Tierpsychol.* **17**: 649–685.

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

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

Engelstädter, J. & Hurst, G.D.D. 2009. The ecology and evolution of microbes that manipulate host reproduction. *Annu. Rev. Ecol. Evol. Syst.* **40**: 127–149.

Fairbairn, D.J., Blanckenhorn, W. & Székely, T. 2007. *Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism*. Oxford University Press, Oxford.

Field, D.L., Pickup, M. & Barrett, S.C. 2013. Comparative analyses of sex-ratio variation in dioecisous flowering plants. *Evolution* **67**: 661–672.

Fisher, R. 1930. *The Genetic Theory of Natural Selection*. Oxford University Press, Oxford.

Fitze, P.S. & Le Galliard, J.F. 2008. Operational sex ratio, sexual conflict and the intensity of sexual selection. *Ecol. Lett.* **11**: 432–439.

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

Fromhage, L., Elgar, M.E. & Schneider, J.M. 2005. Faithful without care: the evolution of monogyny. *Evolution* **59**: 1400–1405.

Griskevicius, V., Tybur, J.M., Ackerman, J.M., Delton, A.W. & Robertson, T.E. 2012. The financial consequences of too many men: sex ratio effects on savings, borrowing and spending. *J. Pers. Soc. Psychol.* **102**: 69–80.

Grubler, M.U., Schuler, H., Muller, M., Spaar, R., Horch, P. & Naef-Daenzer, B. 2008. Female biased mortality caused by anthropogenic nest loss contributes to population decline and adult sex ratio of a meadow bird. *Biol. Conserv.* **141**: 3040–3049.

Gusmao, L.F.M. & McKinnon, A.D. 2009. Sex ratios, intersexuality and sex change in copepods. *J. Plankton Res.* **31**: 1101–1117.

Haig, D. 2006. Evolution, genomic imprinting, and social behavior. *Behav. Genet.* **36**: 967–968.

Hailey, A. & Willemsen, R.E. 2000. Population density and adult sex ratio of the tortoise *Testudo hermanni* in Greece: evidence for intrinsic population regulation. *J. Zool.* **251**: 325–338.

Hardy, I.C.W. 2002. *Sex Ratios: Concepts and Research Methods*. Cambridge University Press, Cambridge.

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

Hirst, A.G., Bonnet, D., Conway, D.V.P. & Kiørboe, T. 2010. Does predation control adult sex ratios and longevities in marine pelagic copepods? *Limnol. Oceanogr.* **55**: 2193–2206.

Hoefler, C.D. 2007. Male mate choice and size-assortative pairing in a jumping spider, *Phidippus clarus*. *Anim. Behav.* **73**: 943–954.

Holland, B. & Rice, W.R. 1999. Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes reproductive load. *Proc. Natl. Acad. Sci. USA* **96**: 5083–5088.

Hunt, G.L. Jr, Wingfield, J.C., Newman, A. & Farner, D.S. 1980. Sex ratio of western gulls on Santa Barbara Island, California. *Auk* **97**: 473–479.

Jennions, M.D. & Kokko, H. 2010. Sexual selection. In: *Evolutionary Behavioral Ecology* (D. Westneat & C. Fox, eds), pp. 343–364. Oxford University Press, New York.

Jirotkul, M. 1999. Operational sex ratio influences female preference and male-male competition in guppies. *Anim. Behav.* **58**: 287–294.

Kalmbach, E. & Benito, M.M. 2007. Sexual size dimorphism and offspring vulnerability in birds. In: *Sex, Size and Gender Roles* (D.J. Fairbairn, W.U. Blanckenhorn & T. Székely, eds), pp. 133–142. Oxford University Press, Oxford.

Karlsson, K., Eroukhmanoff, F. & Svensson, E.I. 2010. Phenotypic plasticity in response to the social environment: effects of density and sex ratio on mating behaviour following ecotype divergence. *PLoS ONE* **5**: e12755.

Keenleyside, M.H.A. 1983. Mate desertion in relation to adult sex ratio in the biparental cichlid fish *Herotilapia multispinosa*. *Anim. Behav.* **31**: 683–688.

Kendall, N.W. & Quinn, T.P. 2013. Size-selective fishing affects sex ratios and the opportunity for sexual selection in Alaskan sockeye salmon *Oncorhynchus nerka*. *Oikos* **122**: 411–420.

Klemme, I., Hannu, Y. & Eccard, J.A. 2007. Reproductive success of male bank voles (*Clethrionomys glareolus*): the effect of operational sex ratio and body size. *Behav. Ecol. Sociobiol.* **61**: 1911–1918.

Klug, H., Alonzo, S.H. & Bonsall, M.B. 2012. Theoretical foundations of parental care. In: *The Evolution of Parental Care* (N. Royle, P. Smiseth & M. Kölliker, eds), pp. 21–39. Oxford University Press, Oxford.

Kokko, H. & Jennions, M. 2008. Parental investment, sexual selection and sex ratios. *J. Evol. Biol.* **21**: 919–948.

Kokko, H., Gunnarsson, T.G., Morrell, L.J. & Gill, J.A. 2006. Why do female migratory birds arrive later than males? *J. Anim. Ecol.* **75**: 1293–1303.

Komdeur, J. 2012. Sex allocation. In: *The Evolution of Parental Care* (N. Royle, P. Smiseth & M. Kölliker, eds), 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. *J. Evol. Biol.* **24**: 1842–1846.

Krumholz, L.A. 1948. Reproduction in the Western mosquitofish, *Gambusia affinis affinis* (Baird & Girard), and its use in mosquito control. *Ecol. Monogr.* **18**: 1–43.

Kusano, T. & Inoue, M. 2011. Adult sex ratio of a population of the Japanese Salamander, *Hynobius tokyoensis* (*Caudata*: *Hynobiidae*). *Curr. Herpetol.* **30**: 129–135.

Kvarnemo, C. & Ahnesjö, I. 1996. The dynamics of operational sex ratios and competition for mates. *Trends Ecol. Evol.* **11**: 404–408.

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

Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. Methuen, London.

Le Galliard, J.F., Fitze, P.S., Ferriere, R. & Clobert, J. 2005. Sex ratio bias, male aggression, and population collapse in lizards. *Proc. Natl. Acad. Sci. USA* **102**: 18231–18236.

Lehikoinen, A., Ost, M., Hollmen, T. & Kilpi, M. 2008. Does sex-specific duckling mortality contribute to male bias in adult common eiders? *Condor* **110**: 574–578.

Lehtonen, J. & Kokko, H. 2012. Positive feedback and alternative stable states in inbreeding, cooperation, sex roles and other evolutionary processes. *Philos. Trans. R. Soc. Lond.* **367**: 211–221.

Liker, A. & Székely, T. 2005. Mortality costs of sexual selection and parental care in natural populations of birds. *Evolution* **59**: 890–897.

Liker, A., Freckleton, R.P. & Székely, T. 2013. The evolution of sex roles in birds is related to adult sex ratio. *Nat. Commun.* **4**: 1587.

Liker, A., Freckleton, R.P. & Székely, T. 2014. Divorce and infidelity are associated with skewed adult sex ratios in birds. *Curr. Biol.* **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.

Lode, T., Holveck, M.J., Lesbarreres, D. & Pagano, A. 2004. Sex-biased predation by polecats influences the mating system of frogs. *Proc. R. Soc. B Biol. Sci.* **271**: S399–S401.

Lovich, J.E. & Gibbons, J.W. 1990. Age at maturity influences adult sex-ratio in the turtle *Malaclemys terrapin*. *Oikos* **59**: 126–134.

Magnhagen, C. 1991. Predation risk as a cost of reproduction. *Trends Ecol. Evol.* **6**: 183–186.

Maly, E. 1970. Influence of predation on the adult sex ratios of two Copepod species. *Limnol. Oceanogr.* **15**: 566–573.

Marchesan, M. 2002. Operational sex ratio and breeding strategies in the Feral Pigeon *Columba livia*. *Ardea* **90**: 249–257.

Mayr, E. 1939. The sex ratio in wild birds. *Am. Nat.* **73**: 156–179.

McKellar, A.E. & Hendry, A.P. 2011. Environmental factors influencing adult sex ratio in *Poecilia reticulata*: laboratory experiments. *J. Fish Biol.* **79**: 937–953.

McKellar, A.E., Turcotte, M.M. & Hendry, A.P. 2009. Environmental factors influencing adult sex ratio in Trinidadian guppies. *Oecologia* **159**: 735–745.

McNamara, J.M., Székely, T., Webb, J.N. & Houston, A.I. 2000. A dynamic game-theoretic model of parental care. *J. Theor. Biol.* **205**: 605–623.

Medrano, M., Alonso, C. & Herrera, C.M. 2005. Mating system, sex ratio, and persistence of females in the gynodioecious shrub *Daphne laureola* L. (*Thymelaeaceae*). *Heredity* **94**: 37–43.

Moore, S.L. & Wilson, K. 2002. Parasites as a viability cost of sexual selection in natural populations of mammals. *Science* **297**: 2015–2018.

Narita, S., Nomura, M. & Kageyama, D. 2007. A natural population of the butterfly *Eurema hecabe* with Wolbachia-induced female-biased sex ratio not by feminization. *Genome* **50**: 365–372.

Osmundson, D.B. 2006. Proximate causes of sexual size dimorphism in Colorado pikeminnow, a long-lived cyprinid. *J. Fish Biol.* **68**: 1563–1588.

Parra, J.E., Beltrán, M., Zefania, S., dos Remedios, N. & Székely, T. 2014. Experimental assessment of mating

opportunities in three shorebird species. *Anim. Behav.* **90**: 83–90.
Pen, I., Uller, T., Feldmeyer, B., Harts, A., While, G.M. & Wapstra, E. 2010. Climate-driven population divergence in sex-determining systems. *Nature* **468**: 436–439.
Pettersson, L.B., Ramnarine, I.W., Becher, S.A., Mahabir, R. & Magurran, A.E. 2004. Sex ratio dynamics and fluctuating selection pressures in natural populations of the Trinidadian guppy, *Poecilia reticulate*. *Behav. Ecol. Sociobiol.* **55**: 461–468.
Pilastro, A., Biddau, L., Marin, G. & Mingozzi, T. 2001. Female brood desertion increases with number of available mates in the rock sparrow. *J. Avian Biol.* **32**: 68–72.
Pitnick, S. 1993. Operational sex-ratios and sperm limitation in populations of *Drosophila pachea*. *Behav. Ecol. Sociobiol.* **33**: 383–391.
Pomfret, J.C. & Knell, R.J. 2008. Crowding, sex ratio and horn evolution in a South African beetle community. *Proc. R. Soc. B* **275**: 315–321.
Post, P. & Gotmark, F. 2006. Foraging behavior and predation risk in male and female Eurasian blackbirds (*Turdus merula*) during the breeding season. *Auk* **123**: 162–170.
Price, T.A.R. & Wedell, N. 2008. Selfish genetic elements and sexual selection: their impact on male fertility. *Genetica* **132**: 295–307.
Prohl, H. 2002. Population differences in female resource abundance, adult sex ratio, and male mating success in *Dendrobates pumilio*. *Behav. Ecol.* **13**: 175–181.
Roff, D.A. 2002. *Life History Evolution*. Sinauer Associates, Sunderland, Massachusetts.
Rossmanith, E., Grimm, V., Blaum, N. & Jeltsch, F. 2006. Behavioural flexibility in the mating system buffers population extinction: lessons from the lesser spotted woodpecker *Picoides minor*. *J. Anim. Ecol.* **75**: 540–548.
Sargeant, A., Allen, S. & Eberhardt, R. 2004. Red fox predation on breeding ducks in midcontinent North-America. *Wildl. Monogr.* **89**: 1–41.
Sauer, E.G.F. 1972. Aberrant sexual behavior in the South African ostrich. *Auk* **96**: 1–5.
Schacht, R., Rauch, K.L. & Mulder, M.B. 2014. Too many men: the violence problem? *Trends Ecol. Evol.* **29**: 214–222.
Schaller, G. 1972. *The Serengeti Lion*. Chicago University Press, Chicago.
Schilthuizen, M., Giesbers, M.C.W.G. & Beukeboom, L.W. 2011. Haldane's rule in the 21st century. *Heredity* **197**: 95–102.
Shuster, S.M. & Wade, M.J. 2003. *Mating Systems and Strategies*. Princeton University Press, Princeton NJ.
Silva, K., Vieira, M.N., Almada, V.C. & Monteiro, N.M. 2010. Reversing sex role reversal: compete only when you must. *Anim. Behav.* **79**: 885–893.
Smith, J.N.M., Yom-Tov, Y. & Moses, R. 1982. Polygyny, male parental care, and sex ratio in song sparrows: an experimental test study. *Auk* **99**: 555–564.
Stamps, J. & Krishnan, V.V. 1997. Sexual bimaturation and sexual size dimorphism in animals with asymptotic growth after maturity. *Evol. Ecol.* **11**: 21–39.
Steifetten, O. & Dale, S. 2012. Dispersal of male ortolan buntings away from areas with low female density and a severely male-biased sex ratio. *Oecologia* **168**: 53–60.
Székely, T., Webb, J.N. & Cuthill, I.C. 2000. Mating patterns, sexual selection and parental care: an integrative approach. In: *Vertebrate Mating Systems* (M. Apollonio, M. Festa-Bianchet & D. Mainardi, eds), pp. 194–223. World Science Press, London.
Székely, T., Moore, A.J. & Komdeur, J. (eds) 2010. *Social Behaviour: Genes, Ecology and Evolution*. Cambridge University Press, Cambridge.
Székely, A. & Székely, T. 2012. Sex ratio and the City. *Curr. Biol.* **22**: 684–685.
Takeshita, F. & Henmi, Y. 2010. The effects of body size, ownership and sex-ratio on the precopulatory mate guarding of *Caprella penantis* (*Crustacea*: *Amphipoda*). *J. Mar. Biol. Assoc. U.K.* **90**: 275–279.
Taylor, D.R. 1999. Genetics of sex ratio variation among natural populations of a dioecious plant. *Evolution* **53**: 55–62.
Tershy, B.R. & Croll, D.A. 2000. Parental investment, adult sex ratios, and sexual selection in a socially monogamous seabird. *Behav. Ecol. Sociobiol.* **48**: 52–60.
Trent, R. & South, S.J. 2011. Too many men? Sex ratios and women's partnering behaviour in China. *Soc. Forces* **90**: 247–267.
Trivers, R. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (B. Campbell, ed.), pp. 136–179. Aldine Press, Chicago.
Trivers, R. 1985. *Social Evolution*. The Benjamin/Cummings Publ Company, Menlo Park, California.
Veran, S. & Beissinger, S.R. 2009. Demographic origins of skewed operational and adult sex ratios: perturbation analyses of two-sex models. *Ecol. Lett.* **12**: 129–143.
Webb, J.N., Székely, T., Houston, A.I. & McNamara, J.M. 2002. A theoretical analysis of the energetic costs and consequences of parental care decisions. *Philos. Trans. R. Soc.* **357**: 331–340.
Wedekind, C., Evanno, G., Székely, T. Jr, Pompini, M., Darbellay, O. & Guthru, J. 2013. Persistent unequal sex ratio in a population of Grayling (*Salmonidae*) and possible role of temperature increase. *Conserv. Biol.* **27**: 229–234.
Weir, L.K., Grant, J.W.A. & Hutchings, J.A. 2011. The influence of operational sex ratio on the intensity of competition for mates. *Am. Nat.* **177**: 167–176.
West, S. 2009. *Sex Allocation*. Princeton University Press, Princeton, NJ.
Whittam, R.M. 1998. Interbreeding of Roseate and Arctic Terns. *Wilson Bull.* **110**: 65–70.
Wigby, S. & Chapman, T. 2004. Female resistance to male harm evolves in response to manipulation of sexual conflict. *Evolution* **58**: 1028–1037.
Wilson, E.O. 1975. *Sociobiology: The New Synthesis*. Harvard University Press, Cambridge, MA.
Young, L.C., Zaun, B.J. & VanderWerf, E.A. 2008. Successful same-sex pairing in Laysan albatross. *Biol. Lett.* **4**: 323–325.

Received 16 December 2013; revised 16 April 2014; accepted 16 April 2014