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Divorce and infidelity are associated with skewed adult sex ratios in birds

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Running head: Divorce and infidelity are related to sex ratio

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Highlights

- Divorce rates are higher in birds with female-biased sex ratios
- Infidelity is more common in male-biased species
- For both sexes the frequency of polygamy is related to adult sex ratio
- The sex ratio is strong driver of many aspects of mating behaviour

Summary

Adult sex ratio (ASR) is a fundamental concept in population demography, and recent theory suggests that ASR plays a central role in social behaviour, mating systems and parental care [1-6]. Unbalanced ASRs are predicted to influence pair-bond and mating behaviour since the rarer sex in the population has more potential partners to mate with than the more common sex [1, 4]. Here we use phylogenetic comparative analyses to test whether ASR is related to three major aspects of mating behaviour: divorce, social polygamy and pair-bond infidelity. ASR is strongly correlated with long-term pair-bonds since divorce rate is higher in species with female-biased sex ratio, indicating that mate change by pair members and/or breaking of pair-bonds by unmated individuals is more frequent when females outnumber males. Short-term pair-bonds are also associated with unbalanced ASRs: males are more commonly polygamous when females outnumber males, and conversely, females are more polygamous when males outnumber females. Furthermore, infidelity increases with male-biased ASR in socially monogamous birds, suggesting that male coercion and/or female willingness to cheat the partner are facilitated by male-biased ASR. Our results provide the first comprehensive support for the proposition that ASR influences multiple aspects of pair-bonds and mating behaviour in wild populations.

Results and Discussion

The significance of adult sex ratios

Adult sex ratio (ASR, defined here as the proportion of adult males in the adult population) is one of the fundamental demographic characteristics that impacts on population growth, demography and extinctions [3, 5, 6]. Recent theoretical models predict that ASR also influences social behaviour including pair-bonds, mating behaviour and parental care [1, 2, 4]. Relationships between ASR and mating behaviour are expected since the members of the rarer sex have more potential partners to mate with, so they may obtain (or change) mate more easily than members of the common sex [1, 2, 4, 7]. For example, in a population with female-biased ASR (i.e. where females outnumber males), males may find partners more quickly than females and may mate with more partners, given the Fisherian condition [8].

Although the theory for linking ASR and mating systems is relatively new, striking examples of the influence of ASR on mating behaviour and pair-bond dynamics have already been found in human societies [9-11]. For instance, divorce rates are higher in countries with female-biased ASR than with male-biased ASR [12], and more frequent divorces are reported in societies having strongly skewed local ASRs (e.g. in workplace), probably due to the higher mating opportunities of members of the rare sex [13, 14]. However, in spite of its theoretical significance, the generality of the relationships between adult sex ratio and components of mating behaviour are largely unexplored in wild populations [15, 16].

We analyse the most comprehensive dataset compiled to date (187 species from 59 families) using the phylogenetic comparative method (Phylogenetic Generalised Least

Squares, PGLS) to test whether variation in ASR is related to interspecific differences in long-term and short-term pair-bonds in birds. ASR may influence long-term pair bonds by altering the frequency (or speed) of pair-bond dissolutions. ASR may also influence short-term pair bonds by altering the frequency of multiple matings, since the rarer sex has more opportunity to mate multiply than the common sex. Although recent models posit that ASR plays a prominent role influencing social behaviour and mating systems [1, 4], we are not aware of any empirical study that comprehensively explored the influences of ASR on both long-term and short-term pair-bonds.

ASR and long-term pair-bonds

Unbalanced ASR can destabilise pair-bonds in two major ways: first, it facilitates the rarer sex in finding a higher quality (e.g. more fertile) mate, that may then induce divorce [17]. Alternatively, the more common sex that experiences a shortage of available partners may harass (or lure away) already mated individuals and thus break up existing pair bonds [18]. Divorce rates (% of pairs that divorce from one year to the next) have an immense range in birds from 0% (e.g. swift *Apus apus*, wandering albatross *Diomedea exulans*) to 100% (house martin *Delichon urbicum,* grey heron *Ardea cinerea*; data from [19]). Although various ecological and life-history traits have been investigated to explain interspecific variation in divorce rates [17, 19, 20], the influence of ASR has not been explored.

Consistently with expectation, divorce is related to ASR: divorce rates are over two times higher in species with female-biased ASR than in male-biased species (Figure 1; mean [± SE] of 100 PGLS models with different phylogenies: slope = -0.239 [0.001], p = 0.013 [<0.001], n = 40 species; see also Figure S1). Furthermore, ASR remains the only significant correlate of divorce when we control for the effects of life-history variables: adult survival, chick development mode and body mass (Table S1A). ASR is also the strongest correlate of divorce when variables previously shown to influence divorce are statistically controlled for [19, 20], including the types of partnership, ornamentation and coloniality (see justification and results in Supplemental Experimental Procedures and Table S1A, respectively). Finally, the significant relationship between divorce and ASR remains when ASR is used as a continuous variable both in bivariate and multi-predictor models (Table S1B), and when phylogenetic multiple imputation is used to eliminate the possible effects of missing data in multi-predictor analyses (Tables S1A & B).

The higher divorce rates in female-biased than in male-biased populations are consistent with the explanation that pair-bonded males initiate divorce more often than pair-bonded females when the ASR is unbalanced. Alternatively, unmated females may be more efficient in breaking up existing pair-bonds in female-biased populations than the unmated males in male-biased populations. Empirical studies support both of these processes. On the one hand, pair-bonded males initiate divorce in blue-footed boobies (*Sula nebouxii*) and in common murres (*Uria aalge*) in response to infidelity of their mates or to acquire a better quality partner [21, 22], and in house wrens (*Troglodytes aedon*) male-initiated mate-switching was more common when unmated females are available [23]. In the aforementioned cases the males deserted their previous mates, established a new territory and/or courted a female, and typically succeeded to breed with a new mate. On the other hand, unmated females can succeed breaking up existing pair-bonds: this may involve harassing established pairs, challenging and fighting with the male's previous mate, and evicting her from the territory [24, 25]. Female harassment was proposed to explain the high divorce rate in a female-biased population of North Island brown kiwis (*Apteryx mantelli*) [18].

ASR and polygamy

Short-term pair-bonds are also related to ASR: males are more polygamous at female-biased ASR than at male-biased ASR (Figure 2A; PGLS, slope = 1.017 [0.004], $p < 0.001$ [<0.001], n = 179 species). Conversely, female polygamy is associated with male-biased ASR (Figure 2B; slope = 0. 259 [0.003], $p = 0.036$ [0.001], n = 179). These results together suggest that at the short term, both males and females respond to improved mating opportunities as indicated by unbalanced ASRs. Furthermore, males are more polygamous relative to females at female-biased ASR than at male-biased ASR (Figure 2C; slope = -1.396 [0.006], $p < 0.001$ [<0.001], n = 179). ASR remains the strongest correlate of polygamy when we control for the effects life-history variables (Table S2A), and for the duration of parental care that was previously suggested to affect avian social mating systems [26] (Table S2A). Finally, the relationship between polygamy and ASR remains highly significant when ASR is used as a continuous variable both in bivariate and multi-predictor models (Table S2B).

These results show that an unbalanced ASR facilitates polygamy by both males and females in a broad range of species, and thus extend previous findings restricted to one avian taxon, the shorebirds [16]. The results are also consistent with observational studies that found increased polygamy at biased adult sex ratios, for example in dunnocks (*Prunella modularis*) [15], blue tits (*Cyanistes caeruleus*) [27] and rock sparrows (*Petronia petronia*) [28]. Furthermore, they are in line with experimental studies in wild populations, since polygamy by males was induced by creating female-biased local ASRs by removing territorial males in willow ptarmigans (*Lagopus lagopus*) and house wrens (*Troglodytes aedon*) [29, 30].

ASR and infidelity

Pair-bond infidelity (i.e. mating with a partner outside the individual's social pair-bond) is common in a wide range of taxa including birds and humans [26, 31, 32]. ASR may influence infidelity in two ways. On the one hand, if infidelity is the consequence of the females' constrained mating options [33], then the frequency of infidelity should decrease with male-biased ASR, because in male-biased populations a female can pair-bond with her preferred male. On the other hand, if infidelity is driven by male coercion through forced copulations [34], or by increased willingness of females when there are more potential males to choose from, then infidelity should increase with male-biased ASR.

Our analyses do not support a general relationship between ASR and infidelity, since they are unrelated in both bivariate (slope = -0.029 [<0.001], $p = 0.726$ [0.004], $n = 89$ species) and multi-predictor analyses including life-history traits and specific traits found to affect the frequency of infidelity, including male care [35-37], male polygamy [33], and clutch size [35] (see rationale and results in Supplemental Experimental Procedures and Table S3, respectively).

However, ASR may influence infidelity differentially in monogamous and polygamous species for two reasons. First, monogamous males may guard their mate more effectively than polygamous males, therefore ASR may have a weaker effect on infidelity in monogamous species than in polygynous ones. Second, females may be less constrained to mate with their preferred mate in polygamous mating systems than in monogamy, therefore ASR may have a weaker influence on infidelity in polygamous species than in monogamous ones [33].

Our results support the latter scenario. ASR and male mating system had an interactive effect on infidelity (PGLS, slope = -0.143, p = 0.007 n = 87 species): in socially monogamous species the frequency of infidelity is significantly higher in species with male-biased than female-biased ASR (Figure 3; slope = 0.336 [<0.001], p = 0.013 [<0.001], n = 51 species), whereas ASR is unrelated to infidelity in polygynous species (slope = -0.168 [0.001], p = 0.143 [0.002], n = 36 species). Furthermore, in monogamous species ASR remains the only significant correlate of infidelity in multi-predictor analyses when we control for the effects of general life-history variables and specific predictors of infidelity (Table S4A). These relationships remain consistent when ASR is modelled as a continuous variable (Table S4B), or when a different cut-off line between monogamous vs. polygynous species (5% male polygamy as opposed to 1% male polygamy) is used in the aforementioned analyses (results not shown). The interaction between ASR and female polygamy on infidelity is not significant (slope= -0.086, p= 0.687, n = 86 species).

To our knowledge, this is the first evidence that male-biased ASR facilitates infidelity in natural populations, primarily in socially monogamous species. Follow-up experimental studies are needed to disentangle whether the relationship between male-biased ASR and infidelity is manifested *via* increased frequency of forced copulations by males, or by allowing females to shop around more extensively for extra-pair partners. Furthermore, studies are needed to investigate males in stable polygynous groups, and mate guarding behaviour of pair-bonded males since mated males may respond to biased ASR by increasing (or relaxing) mate guarding [38].

Adult sex ratios, pair-bonds and infidelity

Taken together, we have shown that both short-term and long-term pair-bonds are related to ASR, although some of these relationships are more complex than theoretical models predicted. For example, infidelity is associated with skewed ASR only in socially monogamous birds. Our results are conceptually important for two reasons. First, they suggest that social environment (as indicated by ASR) may exert a significant influence on divorce, polygamy and infidelity, in addition to ecological and life-history variables that are usually emphasised by behavioural ecologists in the context of mating system evolution [26, 32], and the predictive power of ASR can be substantial [16]. They also demonstrate that both sexes respond to increased mating opportunity, although the higher frequency of male than female polygamy and the higher divorce rate in female-biased than male-biased species may indicate that males generally have a better ability to exploit mating opportunities than females. Second, variations in pair-bonds, sex roles and mating systems are often credited to operational sex ratio (OSR, the ratio of sexually active males to sexually active females) [39, 40]. OSR, however, is not an independent estimate of mating opportunity, since it is influenced by mating behaviour, parental care and post-care refractory periods [39; Székely, T., Komdeur, J. & Weissing, F., unpublished manuscript]. Our results therefore suggest that ASR, a demographic trait derived from juvenile sex ratios, maturation times and sex specific survival of juveniles and adults, appears to exert significant effects on pair bonds, regardless of OSR [4].

In this study we use ASR as predictor and mating behaviours (pair-bonds, infidelity) as responses in the analyses. However, the relationship between these variables may be more complex. Behaviour, for instance competition for mates, may generate skewed ASR through its effects on the mortality of the sexes [41]. Furthermore, there may be feedbacks between ASR and behaviour, resulting in quick parallel changes in ASR, mating behaviour and breeding systems [4, 42, 43]. Experimental manipulations in laboratory and in semi-natural conditions made promising advances toward revealing these relationships [44-49], although further studies are needed to reveal the full implications of the positive and negative feedbacks between ASR and mating behaviour.

Our results in birds show striking parallels with studies in humans: for instance, divorce rates were higher both in birds and humans in female-biased than male-biased populations [12]. ASR is also related to human mating systems, since polygamy by males increases with female-biased ASR [50], and conversely, most cases of polyandry are associated with male-biased ASR [51]. Furthermore, skewed ASR induces increased frequencies of sexual infidelity [52, 53], and sexual coercion by men [11]. Our results in wild populations put forward further topics where ASR research in humans is likely productive. For example, excellent data on human demography would allow researchers to identify the age-cohorts and socio-economic factors that may bias ASR, and to disentangle the complex relationships induced by ASR biases. For instance, sex-biased abortion may lead to heavily male-biased contemporary societies with high rates of rape and extra-pair paternity, with knock on effects on family stability and parental behaviour [10].

Experimental Procedures

We conducted an extensive literature search to collect published and unpublished data on ASR, divorce rates, social polygamy and infidelity from wild bird populations. ASR was commonly estimated in intensively studied breeding populations, although other methods were also used including demographic modeling and counting the sexes in non-breeding populations, or in samples of trapped or dead birds [16]. Annual divorce rate was measured as the percentage of pairs that divorce from one year to the next year in a population. Frequency of social polygamy was estimated for both sexes separately by using a five point scoring system (score 0: $< 0.1\%$, score 4: $> 20\%$ polygamy). We used the frequency of broods containing extra-pair offspring as proxy for infidelity frequency. Sample sizes differ between analyses because not all types of data were available for all species.

We used Phylogenetic Generalized Least Squares (PGLS) with maximum likelihood estimates of Pagel's λ values [54, 55] to analyse interspecific data, as implemented in the R package 'caper' [56]. 100 randomly chosen trees from the most recent global avian phylogenetic hypothesis [57] were used to control for phylogenetic relationships. The full details of the methods are given in the Supplemental Experimental Procedures, and we provide the data set in Table S5.

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Figure legends:

Fig 1. Divorce rates in wild bird populations that exhibit male-biased or female-biased adult sex ratios. Divorce rate (mean ± 1 SE % of pairs that divorce from one year to the next year) is higher in birds with female-biased ASR (proportion of adult males in all adults < 0.5, open bar) than in male-biased species (ASR > 0.5, grey bar; see text for statistics, and Figure S1 and Table S1 for supplemental results).

Fig 2. Adult sex ratio and frequency of polygamous social pair-bonds in birds. (a) In males, polygamy is more frequent in species with female-biased ASR (open bar) than in male-biased species (grey bar), whereas (b) in females polygamy is more frequent when the ASR is male-biased. Polygamy frequency is expressed as score (see Experimental Procedures). (c) Sex difference in polygamy frequencies (polygamy bias, male - female polygamy score) is higher in species with female-biased than with male-biased ASR. Figure shows mean ± 1 SE (see text for statistics, and Figure S1 and Table S2 for supplemental results).

Fig 3. Adult sex ratio, mating system and pair-bond infidelity. In monogamous birds (<1% polygyny, MO), pair-bond infidelity (estimated by the frequency of broods with extra-pair paternity) is higher at male-biased ASR (mb, grey bar) than at female-biased ASR (fb, open bar). In polygynous species (>1% polygyny, PG) the frequency of infidelity does not differ significantly between female-biased and male-biased species. Figure shows mean ± 1 SE (see text for statistics, and Figure S1 and Tables S3-S4 for supplemental results).

Fig 1.

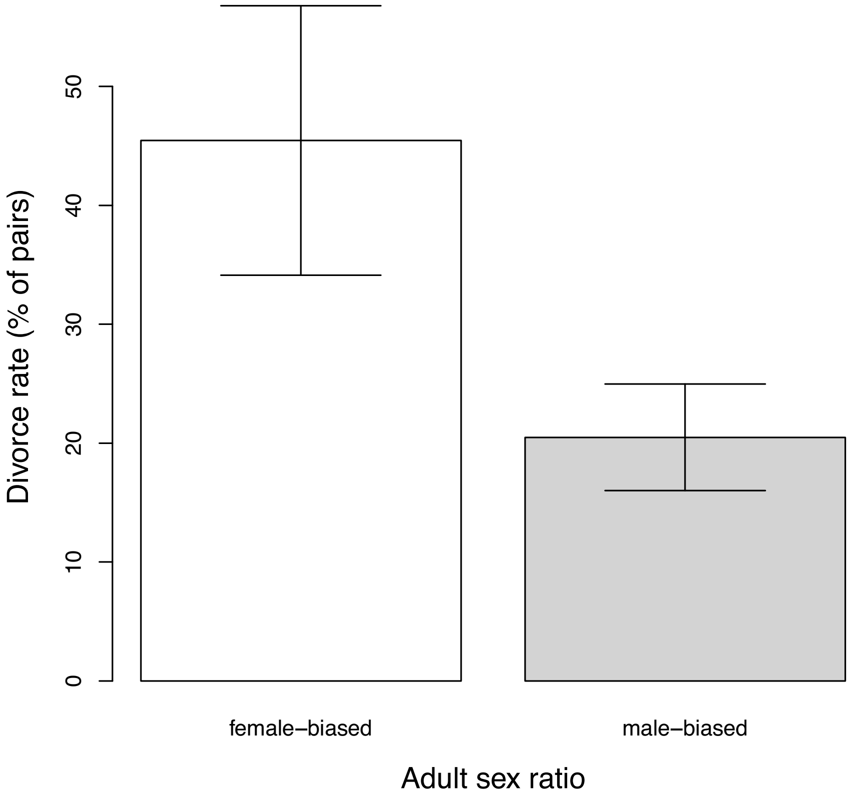
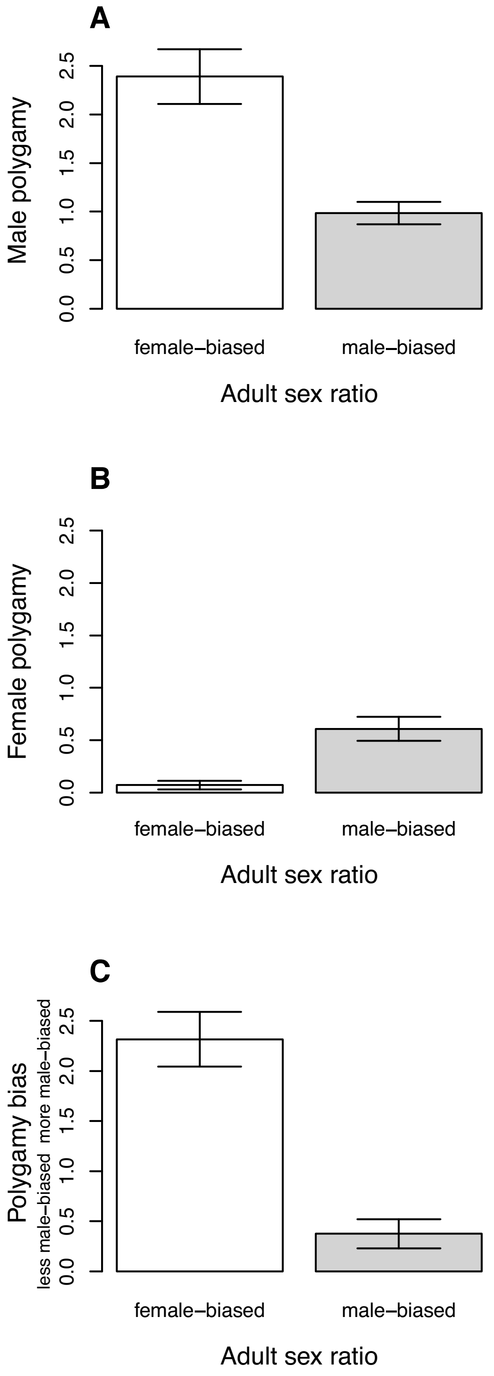

Divorce rate (% of pairs)
0
10
20
30
40
50
female−biased
male−biased
Adult sex ratio

Fig 2.


A
Male polygamy
0.0
0.5
1.0
1.5
2.0
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female–biased
male–biased
Adult sex ratio
B
Female polygamy
0.0
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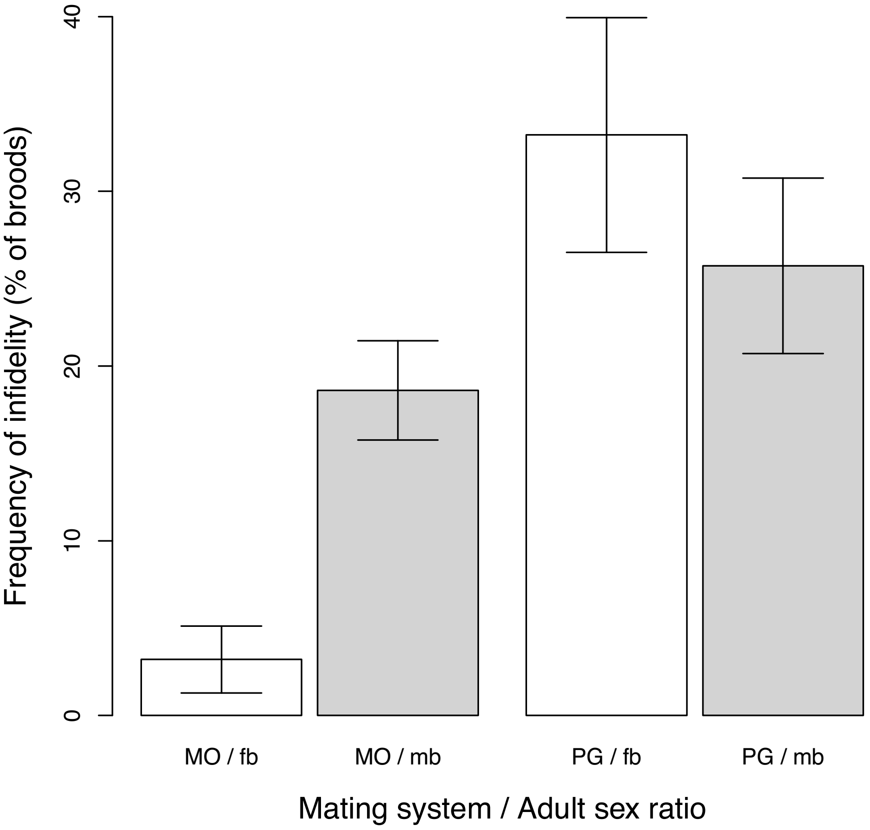
2.5
female–biased
male–biased
Adult sex ratio

Fig 3.


Frequency of infidelity (% of broods)
0
10
20
30
40
MO / fb
MO / mb
PG / fb
PG / mb
Mating system / Adult sex ratio