Report

Divorce and Infidelity Are Associated with Skewed Adult Sex Ratios in Birds

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Summary

Adult sex ratio (ASR) is a fundamental concept in population demography, and recent theory suggests that ASR plays a central role in social behavior, mating systems, and parental care [1–6]. Unbalanced ASRs are predicted to influence pair-bond and mating behavior, 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 behavior: divorce, social polygamy, and pair-bond infidelity. ASR is strongly correlated with long-term pair bonds, since the divorce rate is higher in species with a 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-bond and mating behavior 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 a fundamental demographic characteristic that impacts population growth, demography, and extinction [3, 5, 6]. Recent theoretical models predict that ASR also influences social behavior including pair bonds, mating behavior, and parental care [1, 2, 4]. Relationships between ASR and mating behavior are expected, since the members of the rarer sex have more potential partners to mate with, so they

may obtain (or change) mates more easily than members of the common sex [1, 2, 4, 7]. For example, in a population with a 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 behavior 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 in countries with male-biased ASR [12], and more frequent divorces are reported in societies with strongly skewed local ASRs (e.g., in the workplace), probably due to the higher mating opportunities of members of the rarer sex [13, 14]. However, in spite of its theoretical significance, the generality of the relationships between ASR and components of mating behavior is largely unexplored in wild populations [15, 16].

Here, we analyze the most comprehensive data set compiled to date (187 species from 59 families) using a phylogenetic comparative method (phylogenetic generalized 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 more common sex does. Although recent models posit that ASR plays a prominent role in influencing social behavior and mating systems [1, 4], we are not aware of any empirical study comprehensively exploring the influences of ASR on both long-term and short-term pair bonds.

ASR and Long-Term Pair Bonds

Unbalanced ASR can destabilize pair bonds in two major ways. First, it facilitates the rarer sex in finding a higher-quality (e.g., more fertile) mate, which 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 (percentage of pairs that divorce from one year to the next) have a full range in birds, from 0% (e.g., swift Apus apus, wandering albatross Diomedea exulans) to 100% (house martin Delichon urbicum, gray 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 previously been explored.

Consistent 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 available online). 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
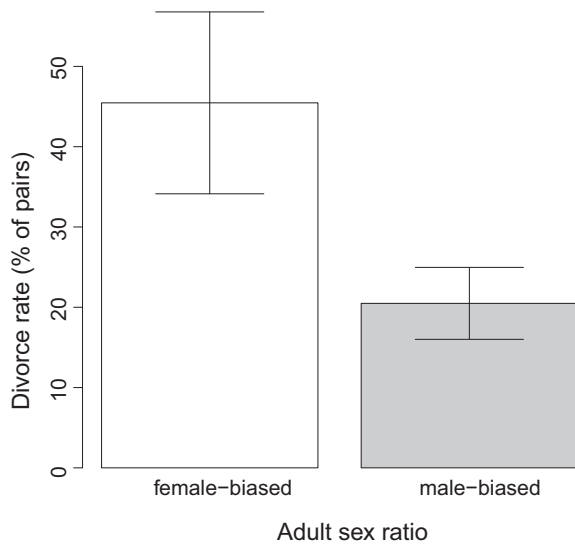
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Figure 1. Divorce Rates in Wild Bird Populations Exhibiting Male-Biased or Female-Biased Adult Sex Ratios

Divorce rate (mean ± SE % of pairs that divorce from one year to the next) is higher in birds with female-biased adult sex ratio (ASR) (proportion of adult males in all adults < 0.5, white bar) than in male-biased species (ASR > 0.5, gray bar; see text for statistics and Figure S1 and Table S1 for supplemental results).

shown to influence divorce are statistically controlled for [19, 20], including the types of partnership, ornamentation, and coloniality (see rationale 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 multipredictor models (Table S1B) and when phylogenetic multiple imputation is used to eliminate the possible effects of missing data in multipredictor analyses (Tables S1A and S1B).

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 with a surplus of the opposite sex. 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 are. Empirical studies support both of these possibilities. 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 by their mates or to acquire a better-quality partner [21, 22], and in house wrens (*Troglodytes aedon*), male-initiated mate switching is 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 in breeding with a new mate. On the other hand, unmated females can succeed in breaking up existing pair bonds: this may involve harassing established pairs, challenging and fighting the male's current mate, and evicting her from the territory [24, 25]. Female harassment has been 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 under female-biased ASR than under 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 in 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 under female-biased ASR than under 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 of 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 in both bivariate and multipredictor 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, shorebirds [16]. The results are also consistent with observational studies finding increased polygamy under biased ASRs, 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 has been induced by creating female-biased local ASRs by removing territorial males in willow ptarmigans (*Lagopus lagopus*) and house wrens [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 females' constrained mating options [33], then the frequency of infidelity should decrease under 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 under 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 multipredictor 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 monogamous ones; 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
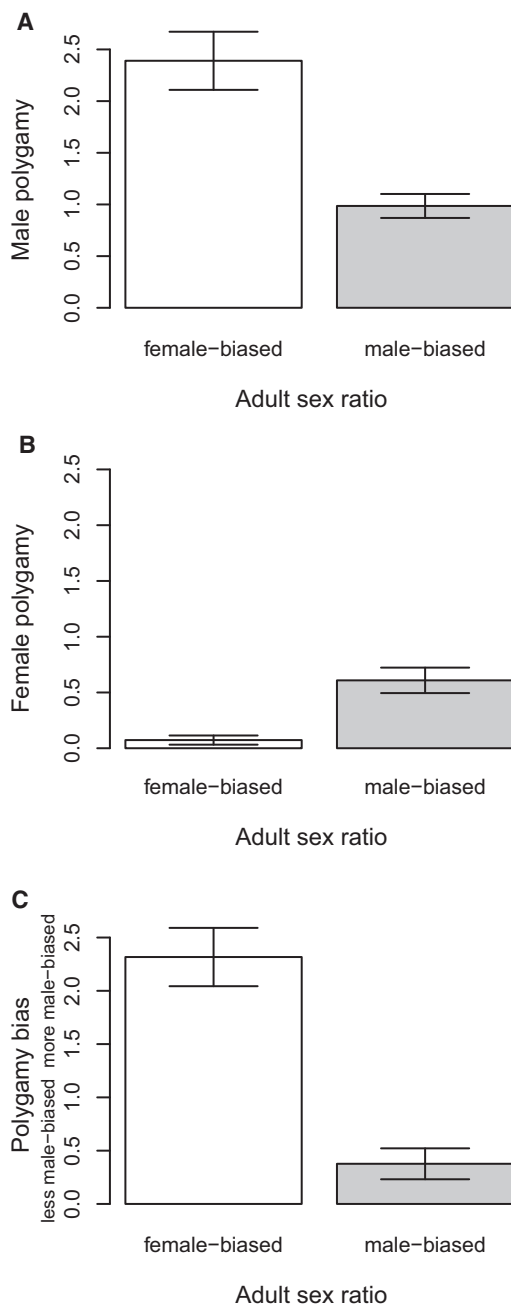
Figure 2. Adult Sex Ratio and Frequency of Polygamous Social Pair Bonds in Birds

(A and B) In males, polygamy is more frequent in species with female-biased ASR (white bar) than in male-biased species (gray bar) (A), whereas in females, polygamy is more frequent when the ASR is male biased (B). Polygamy frequency is expressed on a scale of 0 to 4 (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.

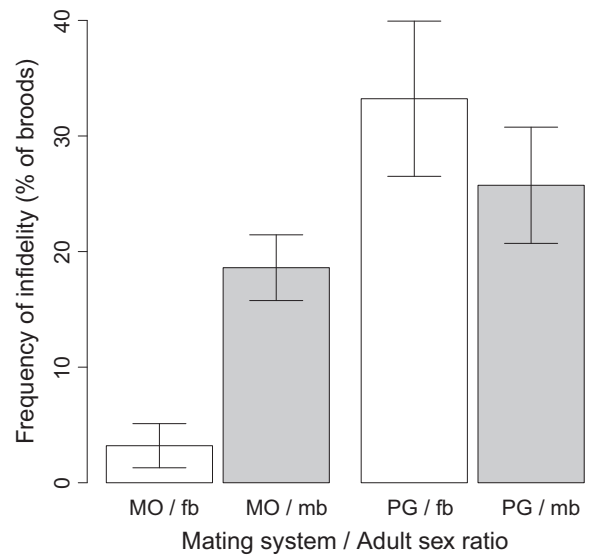Data are means ± SE (see text for statistics and Figure S1 and Table S2 for supplemental results).

Figure 3. Adult Sex Ratio, Mating System, and Pair-Bond Infidelity

In monogamous bird species (<1% polygyny, MO), pair-bond infidelity (estimated by the frequency of broods with extrapair paternity) is higher under male-biased ASR (mb, gray bar) than under female-biased ASR (fb, white bar). In polygamous species (>1% polygyny, PG), the frequency of infidelity does not differ significantly between female-biased and male-biased species. Data are mean ± SE (see text for statistics and Figure S1 and Tables S3 and S4 for supplemental results).

Furthermore, in monogamous species ASR remains the only significant correlate of infidelity in multipredictor 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 modeled as a continuous variable (Table S4B) or when a different cutoff line between monogamous and 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 resolve 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 extrapair partners. Furthermore, studies are needed to investigate males in stable polygynous groups and mate-guarding behavior by 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

Taking together the above results, 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 the ecological and life-history variables that are usually emphasized by behavioral ecologists in the context

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).

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 in male-biased species may indicate that males generally have a better ability to exploit mating opportunities than females do. 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 behavior, parental care, and postcare refractory periods (T.S., J. Komdeur, and F. Weissing, unpublished data). 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 used ASR as a predictor and mating behaviors (pair bonds, infidelity) as responses in our analyses. However, the relationship between these variables may be more complex. Behavior, for instance competition for mates, may generate skewed ASR through its effects on mortality of the sexes [41]. Furthermore, there may be feedbacks between ASR and behavior, resulting in quick parallel changes in ASR, mating behavior, and breeding systems [4, 42, 43]. Experimental manipulations in laboratory and in seminatural conditions have 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 behavior.

Our results in birds show striking parallels with studies in humans. For instance, divorce rates are higher in both birds and humans in female-biased than in male-biased populations [12]. ASR is also related to human mating systems, since polygyny by males increases with female-biased ASR [50], and conversely, most cases of polyandry are associated with male-biased ASR [51]. Furthermore, skewed ASR causes increased frequency of sexual infidelity [52, 53], and sexual coercion by men [11]. Our results in wild populations put forth further topics where ASR research in humans would likely be productive. For example, excellent data on human demography would allow researchers to identify the age cohorts and socioeconomic 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 extrapair paternity, with consequent effects on family stability and parental behavior [10].

Experimental Procedures

We conducted an extensive literature search to collect published and unpublished data on ASR, divorce rates, social polygamy, and infidelity in wild bird populations. ASR was commonly estimated for intensively studied breeding populations, although other methods were also used, including demographic modeling and counting the sexes in nonbreeding populations or in samples of trapped or dead birds [16]. Annual divorce rate was measured as the percentage of pairs that divorced 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% polygamy; score 4, >20% polygamy). We used the frequency of broods containing extrapair offspring as a 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 analyze interspecific data, as implemented in the R package "caper" [56]. One hundred randomly chosen trees from the most recent global avian phylogenetic hypothesis [57] were used to control for phylogenetic relationships.

Full details of our methods are given in the Supplemental Experimental Procedures, and the full data set is provided in Table S5.

Supplemental Information

Supplemental Information includes one figure, five tables, and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.02.059.

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