

Should attractive males have more sons?

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It is often argued that females with attractive partners should produce more sons because these sons will inherit their father's attractiveness. Numerous field and laboratory studies have addressed this hypothesis, with inconsistent results, but there is surprisingly little theoretical work on the topic. Here, we present an extensive investigation of the link between male attractiveness and offspring sex ratios, using evolutionary, individual-based computer simulations. In situations where sexual selection leads to the stable exaggeration of a costly male trait and a costly female preference, we find that females with attractive partners produce more sons than females with unattractive partners. This same qualitative pattern is seen for a wide range of different models, with discrete or continuous variation in the male trait, under Fisherian or good-genes sexual selection and for abrupt or gradual sex ratio adjustment. However, in all simulations, it takes a huge number of generations to evolve, suggesting that selection acting on sex ratio adjustment is weak. Our models ignore many potential costs and constraints associated with manipulation, which implies that selection may be weaker still in natural populations. These results may explain why published evidence for sex ratio bias in relation to male attractiveness is mixed. *Key words:* attractiveness, Fisherian runaway, good genes, handicap principle, individual-based simulation, sex allocation, sex ratio, sexual selection, Trivers–Willard hypothesis. [*Behav Ecol*]

Whether animals adaptively adjust the sex ratio of their offspring (Trivers and Willard 1973) is currently one of the hottest topics in behavioral ecology. Sex-allocation theory has met with considerable success when applied to haplodiploid insects (Godfray and Werren 1996), but the evidence in vertebrates with chromosomal sex determination is controversial and has attracted a number of recent, high-profile reviews and meta-analyses (e.g., Komdeur and Pen 2002; West and Sheldon 2002; Ewen et al. 2004; Sheldon and West 2004; Cassey et al. forthcoming). For mammals and birds, in particular, very little is understood about the possible mechanisms of sex ratio adjustment (Krackow 1995; Pike and Petrie 2003), and this fact is compounded by often weak and inconsistent patterns reported in the literature (Ewen et al. 2004; Sheldon and West 2004; Cassey et al. forthcoming).

One influential idea in this research area is that females mated to attractive males should produce more sons because these sons will inherit their father's attractiveness and enjoy high mating success, thereby yielding greater fitness returns than daughters. This verbal argument was originally developed by Burley (1981, 1986) in her classic work on zebra finches (*Taeniopygia guttata*) and has been restated in numerous subsequent papers by others (e.g., Ellegren et al. 1996; Radford and Blakey 2000; Dreiss et al. 2005; Edvardsson and Arnqvist 2005). It has commonly been investigated in birds, in which the males often show obvious sexually selected traits (Darwin 1874; Andersson 1994) and females, as the heterogametic sex, potentially have control over offspring sex (Krackow 1995). In mammals, in contrast, many of which live in highly structured societies, patterns of sex ratio variation have been related more to maternal condition or dominance rank (Cockburn et al. 2002; Sheldon and West 2004).

Despite considerable research effort, the evidence for a link between offspring sex ratios and paternal attractiveness is mixed. For example, Sheldon et al. (1999) reported experimental evidence that brood sex ratios in wild blue tits (*Parus*

caeruleus) were biased in response to the ultraviolet reflectance of the male's crown feathers, a known sexually selected trait. Griffith et al. (2003) found correlative evidence in support of this from the same population, but Dreiss et al. (2005) found no association between male plumage color and offspring sex ratios in a different population, and Korsten et al. (2006), in a faithful replication of the study of Sheldon et al. (1999), found an association in only one out of 2 years. Results from other species have been similarly variable, some studies (e.g., Pike and Petrie 2005) finding strong support for the hypothesis, some (e.g., Parker 2005) casting doubt on previously published evidence, and others suggesting that patterns of adjustment are not consistent across populations (Rosivall et al. 2004) or years (Radford and Blakey 2000). Even the findings of Burley (1981, 1986) in zebra finches, which initiated this research area, have not been replicated in other studies (Zann and Runciman 2003; Rutstein et al. 2004, 2005), including one following the same experimental design (Von Engelhardt et al. 2004).

Given the prominence of this topic and the inconsistency in results, it is surprising that so little theoretical work exists to complement the published experiments. Several authors (e.g., Leimar 1996; Wade et al. 2003) have investigated the effect of maternal condition on offspring sex ratios, revealing some interesting caveats to the hypothesis of Trivers and Willard (1973), but only one study (Pen and Weissing 2000) has addressed the link between offspring sex ratios and paternal attractiveness. The evolutionarily stable strategy (ESS) approach of Pen and Weissing (2000) suggested that, when subjected to a formal theoretical analysis, the verbal reasoning that attractive males should have more sons might not be so straightforward. First, an association between male attractiveness and offspring sex ratios depends on whether the female preference is for an arbitrary "Fisherian" trait or an indicator of "good genes." Consistent sex ratio biases are expected in a good-genes model but not in a pure Fisherian model with no cost to female choice and unbiased mutations on the male trait. Second, the pattern of sex ratio adjustment seen in the good-genes model differs from that in the common verbal argument: females with attractive partners should in fact produce a roughly even sex ratio, whereas those with unattractive partners should overwhelmingly produce daughters. However, although the analysis of Pen and Weissing provided some important insights, their simplified approach considered only

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2 types of males, “attractive” males and “unattractive” males. In reality, male attractiveness is likely to vary along a continuum (Andersson 1994; Grant PR and Grant BR 1997).

Here, we provide an extensive theoretical investigation of the link between male attractiveness and offspring sex ratios, using evolutionary, individual-based computer simulations. These simulations are complementary to the ESS analysis of Pen and Weissing (2000) and also allow us to model complex situations that are beyond the reach of analytical techniques. Our general approach involves first simulating the evolution of a conspicuous male trait and female preference according to standard models of sexual selection then incorporating into this model the possibility for females to determine the sex of their offspring.

We present 2 main models, differing in the form of the male trait. Model 1 considers discrete variation, with males either possessing or lacking the trait (as in Pen and Weissing 2000). This is based on the 2-locus genetic model of Kirkpatrick (1982) and the 3-locus models of Maynard Smith (1985), Kirkpatrick (1986), and Pomiankowski (1988). Model 2 considers a continuously variable male trait and is based on the quantitative genetic models of Iwasa et al. (1991) and Pomiankowski et al. (1991). For each model, we consider the 2 classic forms of sexual selection (Andersson 1994): Fisherian “runaway” selection, in which males vary in attractiveness but not in heritable viability, and good-genes selection, in which variation in heritable viability is included.

MODEL 1: DISCRETE VARIATION IN MALE TRAIT

The model

We consider a sexually reproducing population of males and females, each with 5 genetic loci of interest: a trait locus T (with alleles t_0 and t_1), a preference locus P (alleles p_0 and p_1), a viability locus V (alleles v_0 and v_1), and 2 sex ratio loci S_0 and S_1 (many possible alleles). Males with allele t_1 express a conspicuous trait, for example, elongated tail feathers, and pay an associated survival cost relative to males with allele t_0 , who do not express the trait. Females with allele p_1 prefer to mate with trait-bearing males and pay a survival cost for being choosy, whereas those with allele p_0 have no preference and mate randomly. Males and females with allele v_0 have reduced premating survival compared with those with allele v_1 (for the results we present, the survival reduction was 1/6). The sex ratio loci S_0 and S_1 are expressed in females and determine the probability of producing a son when mated to a trait-bearing male (S_1) or a traitless male (S_0). We consider a large number of alleles at these 2 loci, coding for any probability between 0 (exclusively daughters) and 1 (exclusively sons) in steps of 1/250.

Each mating produces a single offspring, which inherits alleles from its parents in a simple Mendelian fashion. We assume a small frequency of mutation at the sex ratio loci S_0 and S_1 , causing their value to change up or down by 1/250. Mate search and reproduction continue until the number of female offspring produced is equal to the number of females in the adult population. When this point is reached, all adult individuals die and are replaced by the offspring generation (i.e., generations are nonoverlapping).

In the Fisherian version of our model, we eliminate all variation in heritable viability (i.e., at the V locus) and introduce recurrent deleterious mutations at the T locus, such that a small frequency of inherited t_1 alleles mutate into t_0 . Recurrent deleterious mutations are a standard ingredient of genetic models of sexual selection (Maynard Smith 1991) and prevent t_1 from going to fixation, thereby maintaining variability among males (Charlesworth 1987). For direct comparison with the analysis of Pen and Weissing (2000), we also

consider a “pure” Fisherian model without such mutations. In the good-genes version of our model, we allow variation in V and assume recurrent deleterious mutations at this locus, rather than at T . In line with previous good-genes models (e.g., Maynard Smith 1985; Pomiankowski 1988; Andersson 1994), we investigate different forms of the trait: if it is a “pure epistatic indicator,” all males with allele t_1 express the trait; if it is a “conditional indicator,” only those with both t_1 and v_1 express it (for further details, see Andersson 1994). A “revealing indicator,” in which all males with t_1 express the trait but only those that also have v_1 are preferred by choosy females, yielded virtually identical results to the conditional indicator, so we do not discuss this further.

Our simulations were implemented in Pascal and C++ programming languages. Copies of the code are available from the authors on request.

Results

We present the results for a population of 4000 females and a variable number of males (initially also 4000). Data are given as mean values \pm standard error from 10 replicate simulation runs.

Coevolution of male trait and female preference

Male trait and female preference coevolve in the standard way predicted by analytical models of sexual selection (summarized by Maynard Smith 1991; Andersson 1994). Above some threshold frequency of the female preference (p_1), the trait allele t_1 spreads rapidly at first: within 50 generations, the frequency of trait-bearing males rises from 1% to over 80%. Under Fisherian sexual selection, this spread is only stable when there are recurrent deleterious mutations on the trait (frequency of t_1 after 500 generations = 0.83 ± 0.003); otherwise, any cost to female choice causes both trait and preference to go to extinction. Deleterious mutations prevent t_1 from reaching a frequency where trait-bearing and traitless males are equally fit and thereby maintain the benefit of female choice. Under good-genes sexual selection, costly female choice maintains the male trait if it is a conditional indicator (t_1 fixated within 500 generations) but not if it is a pure epistatic indicator (t_1 extinguished within 500 generations). This set of results is well known to researchers working on sexual selection (Andersson 1986, 1994; Pomiankowski 1988; Maynard Smith 1991).

Sex ratio adjustment

We consider the evolution of sex ratio adjustment in all cases where the male trait allele t_1 persists (pure Fisherian trait; Fisherian trait plus mutation bias; conditional indicator). Change at the sex-allocation loci S_0 and S_1 is summarized in Figure 1. In a pure Fisherian model (no mutations at T and no cost to female choice), sex ratio adjustment does not evolve, as predicted by Pen and Weissing (2000). Trait-bearing males have no net fitness advantage in this scenario (because their greater mating success is counterbalanced by reduced survival), so this result is not surprising.

For a conditional indicator or a Fisherian trait subject to recurrent deleterious mutations, however, sex ratio adjustment based on male attractiveness gradually develops (Figure 1, middle and bottom panels). In a twist to the common verbal argument, females mated to trait-bearing (attractive) males do not overproduce sons; rather, those mated to traitless (unattractive) males overproduce daughters. This fits nicely with the analytical work of Pen and Weissing (2000), who predicted that a bias in the sex ratio related to male attractiveness would lie primarily with the females with unattractive partners, not those with attractive partners. The explanation for the pattern is that the vast majority of males possess the trait, and so a strong sex ratio

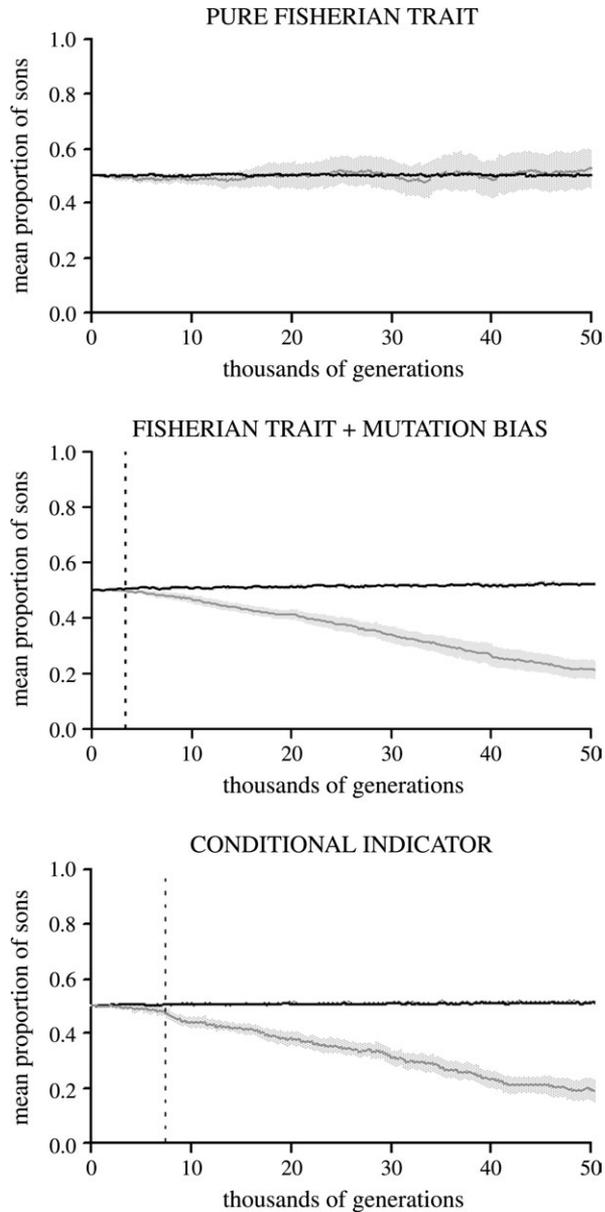


Figure 1
Evolution of sex ratio adjustment for 3 different forms of a conspicuous male trait showing discrete variation (Model 1). Plots show the average proportion of sons produced by females mated to trait-bearing males (locus S_1 , black line) and traitless males (locus S_0 , gray line), given as mean (solid line) \pm standard error (stippling) from 10 replicate simulation runs. Vertical dotted lines indicate points beyond which the 2 sex ratios are significantly different (paired t tests, $P < 0.05$).

bias in their offspring is likely to be counteracted by selection pressures favoring the rarer sex, which tend to preserve a roughly even population sex ratio (Fisher 1930). In contrast, sex ratio bias in the few females with traitless partners has a limited effect on the population sex ratio. These females are selected to overproduce daughters because sons will lack the trait and therefore suffer a mating disadvantage.

However, this pattern of sex ratio adjustment takes tens of thousands of generations to develop. Compared with selection on the conspicuous male trait, which reaches a stable frequency within 300 generations, selection on sex ratio adjustment appears to be rather weak.

MODEL 2: CONTINUOUS VARIATION IN MALE TRAIT

The model

In Model 2, the conspicuous male trait is not binary (e.g., elongated tail either present or absent) but can take a continuous range of values (e.g., precise length of tail). Heritable viability, female preference, and the traits determining sex allocation also show continuous variation. To model this in an individual-based simulation, we give each individual a “genetic value” for each trait, which can be any real number within a certain range. Offspring values are calculated as the average of the maternal and paternal values, though in a small frequency of offspring these change up or down through mutation. A mechanistic interpretation of this would be that each trait is coded by a single locus, each with an infinite number of alleles. However, we expect that the patterns we observe would be no different if each trait was in fact influenced by many different loci (i.e., polygenic), each with a small effect and interacting in an additive fashion. Our predictions can therefore be compared with those from quantitative genetic models of sexual selection (Mead and Arnold 2004).

We based our simulations on the classic quantitative genetic models of Iwasa et al. (1991) and Pomiankowski et al. (1991). As for Model 1, we present 2 main scenarios, one implementing Fisherian sexual selection (in accordance with Pomiankowski et al. 1991) and the other implementing good-genes sexual selection (in accordance with Iwasa et al. 1991). In each case, we first consider the evolution of the male trait and female preference in the absence of variation in offspring sex ratios to assess the extent to which our simulations support the predictions of the analytical models of Iwasa et al. (1991) and Pomiankowski et al. (1991). We then incorporate the possibility of sex ratio adjustment and investigate whether this becomes associated with male trait expression.

Trait values and heritable viability

We consider a sexually reproducing population of N individuals, each with genetic values t (male trait), p (female preference), and v (heritable viability). Males express the trait but not the preference, whereas females express the preference but not the trait, although both sexes carry genes for both trait and preference.

Heritable viability v influences survival to maturity in both sexes and can take any value between 0 (minimum viability) and 1 (maximum viability). In the Fisherian version of our model, we eliminate variation in heritable viability by giving all individuals the same value of v and setting the mutation rate on this trait to zero. In the good-genes version, in contrast, we allow v to vary and assume a certain frequency of mutations, drawn from a negative exponential probability distribution (after Iwasa et al. 1991). These mutations keep the mean value of v below its maximum, maintaining variation in heritable viability between males.

Male trait and survival to maturity

The genetic value t determines a male’s potential trait expression, but how this translates into realized (phenotypic) trait expression depends on the type of trait we are considering. In all cases, we use x to denote the trait phenotype, with this directly influencing survival and mating success. For a Fisherian trait and a pure epistatic indicator, $x = t$, such that all males with the same value of t express the trait to exactly the same extent (e.g., have the same tail length), regardless of any differences in heritable viability. For a conditional indicator, in contrast, both t and v determine the phenotype of the trait according to the function $x = tv$. Thus, males of higher genetic viability express the trait more strongly for a given value of t . For example, if tail length is a conditional indicator,

males of higher viability will grow longer tails than males with the same potential trait value (t) but lower viability. (The same results were obtained for a revealing indicator, so we do not discuss this further.)

After Pomiankowski et al. (1991), we set the survival optimum for the trait phenotype at a value of $x = 0$. In terms of our example, $x = 0$ represents the tail length that optimizes flight performance, escape from predators, and so on. Male survival decreases either side of this optimum (i.e., for both longer and shorter tails) according to the function $\exp(-cx^2)$, where c is a positive constant. However, female choice (described below) may drive the male trait away from the survival optimum in either direction, leading to positive or negative trait values. The likelihood that a male will reach reproductive maturity therefore depends on both heritable viability and expression of the trait and is calculated as $v \cdot \exp(-cx^2)$.

Female preference and survival to maturity

A female's preference is determined by her genetic value for p . A value of $p < 0$ indicates preference for lower phenotypic trait values, whereas $p > 0$ indicates preference for higher values; a female with $p = 0$ mates at random (Pomiankowski et al. 1991). Because choosiness over mates is likely to entail costs, we assume a decrease in female survival either side of $p = 0$, according to the function $\exp(-bp^2)$, where b is a positive constant scaling the cost of choice. Female survival is also influenced by heritable viability v and is calculated as $v \cdot \exp(-bp^2)$.

For each mating event, a female is drawn from the population at random with a chance proportional to her survival probability. To select a father for each of her offspring, the female randomly samples n males and chooses one of them on the basis of his trait expression. (We present the results for $n = 10$, but changing this to $n = 5$ or $n = 20$ did not affect the outcome.) The probability a given male in the sample will be chosen is weighted by the function $\exp(afx)$, where a is a positive constant scaling the importance of the male trait to female choice. Thus, if the female in question has a preference of $p < 0$, such that she favors males with below-average trait expression, those males with more negative values of x (e.g., shorter tails) will be more likely to mate. Conversely, if she favors males with above-average trait expression ($p > 0$), those males with more positive values of x (e.g., longer tails) will be more likely to mate. If the female has no preference ($p = 0$), each male in the sample has an equal chance of being selected.

Each mating produces a single offspring. Reproduction continues until the number of offspring equals the size of the adult population (N), at which point all the adults die and are replaced by the offspring generation.

Sex allocation

Building on these standard models of sexual selection, we then allow mothers to influence the sex ratio of their offspring. We explore 2 possibilities for this, one a "bang-bang" strategy with an abrupt switch between 2 sex ratios and the other permitting more gradual adjustment. In the former case, we incorporate 2 sex-allocation traits s_+ and s_- , which can take any real value between 0 and 1. For any given mating, offspring sex is determined by the mother's values of s_+ and s_- ; the father's sex-allocation genes are assumed to have no influence. The s_+ specifies the probability of producing a son when mated to a male whose trait expression (x) is above average, whereas s_- specifies the probability of producing a son when mated to a male whose trait expression is below average. This requires that females have some way of knowing the average male phenotype \bar{x} , a point we will return to in the Discussion.

The alternative, more gradual, form of adjustment also involves 2 sex-allocation traits, this time α and β , which can take

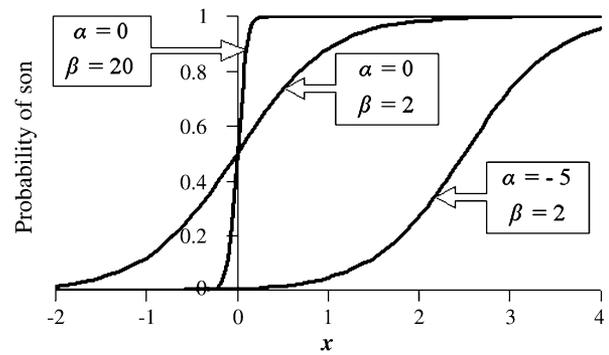


Figure 2

Three possible strategies of maternal sex allocation in relation to male phenotype (x) and their associated values of the sex-allocation traits α and β . The probability of producing a son is given by the logistic function $(1 + \exp[-(\alpha + \beta x)])^{-1}$, where the genetic values of α and β are free to evolve through mutation and selection. Negative values of β (not shown) are also possible, leading to a decrease in the probability of a son with male phenotype x . All simulations started with $\alpha = \beta = 0$, which gives a flat line of height 0.5 (even sex allocation, regardless of male phenotype).

any real value (positive or negative). The probability that the offspring will be male is given by the logistic function $(1 + \exp[-(\alpha + \beta x)])^{-1}$, which implies that sex allocation will be related to the father's trait phenotype provided $\beta \neq 0$. Three examples of the form of this function are depicted in Figure 2. Higher values of β give a steeper relationship between x and the sex ratio, with $\beta = \pm \infty$ implying an extreme type of bang-bang strategy in which the probability of a son switches suddenly between 0 and 1. The α determines the value of x for which a 50:50 sex ratio is produced.

Compared with bang-bang adjustment, the logistic function allows greater flexibility in the sex-allocation strategy and a more subtle response to the male trait. On the other hand, the former is more straightforward to analyze and allows the 2 sex-allocation traits to evolve independently of each other.

Mutation

For each trait (except for v in the Fisherian version of the model), we assume that mutations occur in small proportion of offspring, changing their genetic value for that trait. Changes can occur in either direction but may have a downward bias, such that mutations are more likely to reduce the genetic value than increase it. Where we have implemented a downward mutation bias, this is in line with standard models of sexual selection (Andersson 1994) and, like the recurrent deleterious mutations in Model 1, is important for maintaining fitness differences between males (Charlesworth 1987). Moreover, it has been argued that the fitness consequences of random mutations in a complex trait, such as viability or a conspicuous male ornament, are much more likely to be detrimental than beneficial (Pomiankowski et al. 1991).

Mutations in p and t occur in proportions μ_P and μ_T of offspring, respectively, and cause the genetic value to change by an amount drawn from a uniform probability distribution (up to a certain maximum amount). For p , upward and downward changes are equally likely (i.e., mutations are unbiased), and hence their average effect in an individual offspring is zero. For t , we represent the average downward effect of mutations by the parameter u . In the Fisherian version of the model, these may be biased ($u > 0$), whereas in the good-genes model, they are always unbiased ($u = 0$). In the good-genes model, mutations also occur in v in a proportion μ_V of

offspring and change the genetic value by an amount drawn from a negative exponential distribution (as in Iwasa et al. 1991). These mutations have a net downward effect, with the average decrease in v represented by the parameter w ($w > 0$). In both Fisherian and good-genes models, mutations in the sex-allocation traits appear at a frequency of μ_S in the offspring and are unbiased.

Results

We present the results for a fixed population size of $N = 5000$ individuals, initially with equal numbers of males and females. Simulations were run for 50 000 generations, over which we monitored the changing mean values for potential trait expression t , preference p , viability v , and the sex-allocation traits (s_+ and s_- or α and β , depending on the version of the model). The patterns were similar regardless of the initial conditions, but for the purpose of comparison, we present here the results of simulations with starting values $\bar{t} = 0$, $\bar{p} = 3$ and, for the good-genes versions, $\bar{v} = 0.01$. All mothers in the first generation produced sons and daughters with equal probability ($\alpha = \beta = 0$ or $s_+ = s_- = 0.5$). Values for parameters not mentioned below were as follows: $a = 1.0$, $c = 0.5$, $\mu_P = \mu_T = \mu_V = 0.05$. For the simulations allowing sex ratio adjustment, we changed the mutation rate in the sex-allocation traits from $\mu_S = 0$ to $\mu_S = 0.05$. Despite small fluctuations, the population sex ratio never became more skewed than 42.4% males (2881 females and 2119 males) or 56.3% males (2187 females and 2813 males).

Coevolution of male trait and female preference

The simulation results fit well with the analytical predictions of the quantitative genetic approach of Iwasa et al. (1991) and

Pomiankowski et al. (1991). In a pure Fisherian model with no cost to female choice ($b = 0$) and no mutation bias on the male trait ($u = 0$), trait and preference values evolve toward a line of equilibria where the degree of trait exaggeration balances the associated survival cost with the mating advantage (Figure 3, top left). The equilibria on this line are unstable: incorporating even a small cost of choice ($b = 0.001$) drives trait and preference to their survival optima (not shown). A downward mutation bias ($u = 0.008$) rescues this process and allows stable exaggeration of the trait, this time with a single equilibrium point rather than a line of equilibria (Figure 3, top right).

In the good-genes model, stable exaggeration of a costly male trait and costly female preference ($b = 0.0025$) is only possible if there is a downward mutation pressure on heritable viability ($w = 0.02$). This keeps \bar{v} just below its maximum value, thereby ensuring that a female who chooses at random will, on average, obtain a mate of lower viability than one who chooses on the basis of a sufficiently reliable indicator trait. Even with this effect of mutation, stable exaggeration will occur only for a conditional indicator, not for a pure epistatic indicator (Figure 3, bottom panels). For this reason, we do not consider sex ratio adjustment for a pure epistatic indicator.

Bang-bang sex ratio adjustment (traits s_+ and s_-)

As for the discrete-trait model, evolution of sex ratio adjustment proceeds slowly. For a pure Fisherian model, females whose partners have below-average trait expression initially develop a slight (nonsignificant) bias toward daughters, but this pattern subsequently disappears (Figure 4, top). With costly choice and a mutation bias on the male trait, however, a clear pattern emerges: females mated to attractive males overproduce sons, whereas those mated to unattractive males

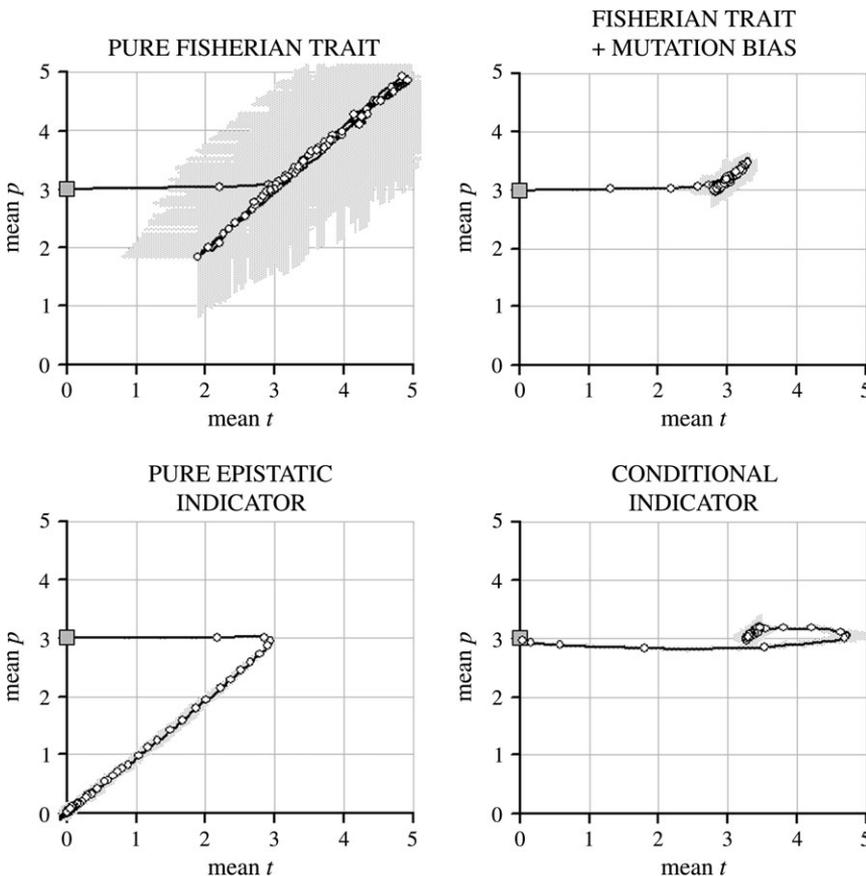


Figure 3

Coevolution of a female preference and a conspicuous male trait showing continuous variation (Model 2) for 4 different forms of the male trait. Plots show population mean values for the female preference (p) and male trait (t) over 5000 generations of selection, with sex ratio adjustment able to evolve ($\mu_S = 0.05$). The starting point of the simulations is indicated by a gray square; open circles mark intervals of 50 generations. Data are given as mean (solid line) \pm standard error (stippling) from 10 replicate simulation runs. Parameter values are given in the main text.

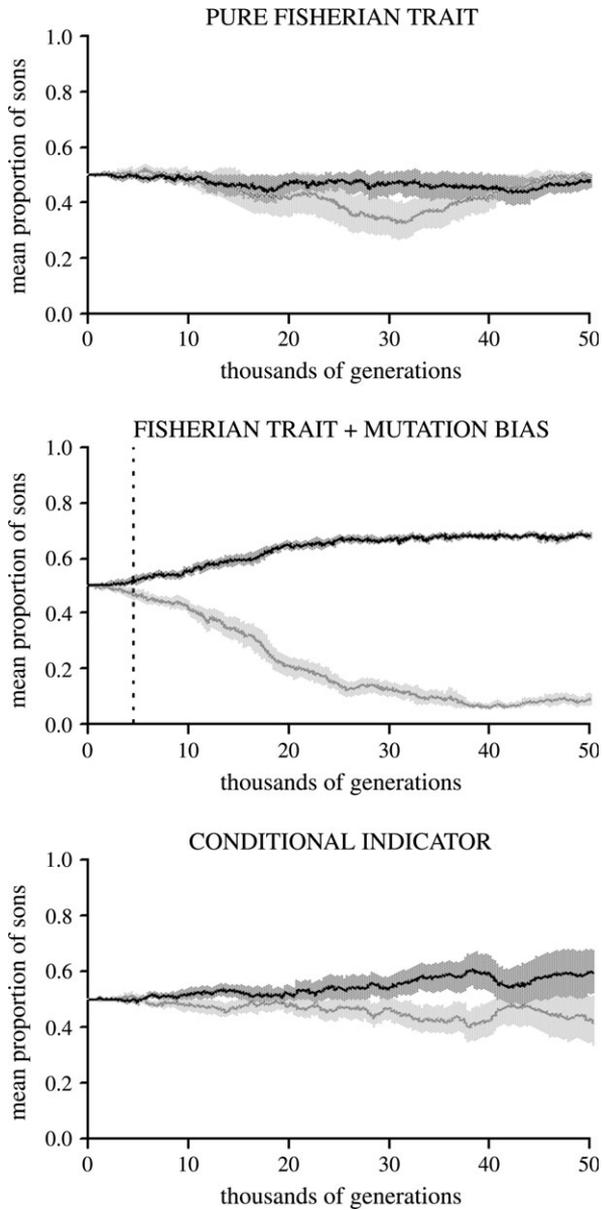


Figure 4
Evolution of sex ratio adjustment for 3 different forms of a conspicuous male trait showing continuous variation (Model 2). Plots show the average proportion of sons produced by females mated to males with above-average (s_+ , black line) and below-average (s_- , gray line) trait expression, given as mean (solid line) \pm standard error (stippling) from 10 replicate simulation runs. Vertical dotted lines indicate points beyond which the 2 sex ratios are significantly different (paired t tests, $P < 0.05$). Parameter values are given in the main text.

overproduce daughters (Figure 4, middle). These sex ratio biases take 40 000 generations to reach their full extent.

When the male trait is a conditional indicator of good genes, the sex ratio biases that evolve are slight and show some inconsistency between simulation runs. Females mated to attractive partners (above-average x) produce slightly more sons than those mated to unattractive partners (below-average x), but this difference is not significant (Figure 4, bottom).

Gradual sex ratio adjustment (traits α and β)

Similar results emerge for the alternative form of sex ratio adjustment. The sex-allocation traits α and β show significant

divergence from their starting values of 0 only in the case of a Fisherian trait with costly choice and biased mutations, with α gradually decreasing and β gradually increasing (Figure 5, middle). The positive value of β indicates that, on average, more sons are produced for higher values of the father's trait phenotype x . The precise pattern of sex ratio adjustment differs slightly between simulation runs; the data from one simulation are shown as an example in Figure 6. Here, contrary to the results from Model 1, offspring sex ratios are biased to a similar extent by females with attractive and unattractive partners.

Sex ratio adjustment for a conditional indicator is less clear and shows high variability between simulation runs (Figure 5, bottom; note the large standard errors). Attractive males do have slightly more sons on average: considering only those matings involving the top 10% and bottom 10% of male trait phenotypes (x), the proportion of sons in the 50 000th generation is, respectively, 0.68 ± 0.082 and 0.32 ± 0.091 .

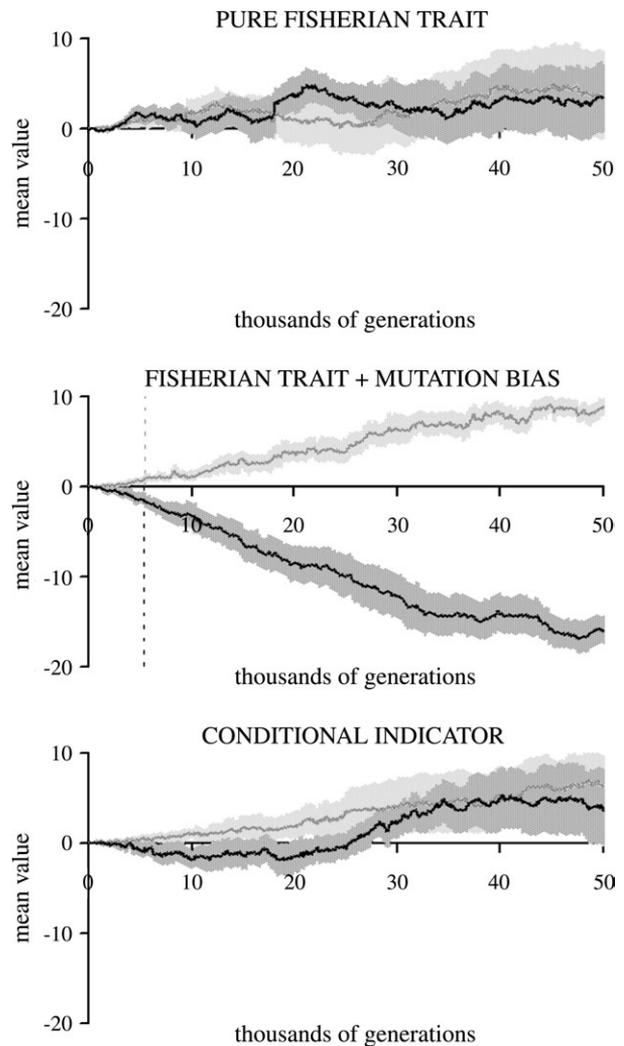


Figure 5
Evolution of sex ratio adjustment for 3 different forms of a conspicuous male trait showing continuous variation (Model 2). Plots show population mean values for sex-allocation traits α (black line) and β (gray line), given as mean (solid line) \pm standard error (stippling) from 10 replicate simulation runs. Vertical dotted lines indicate points beyond which the trait value is significantly different from zero (1-sample t tests, $P < 0.05$). Parameter values are given in the main text.

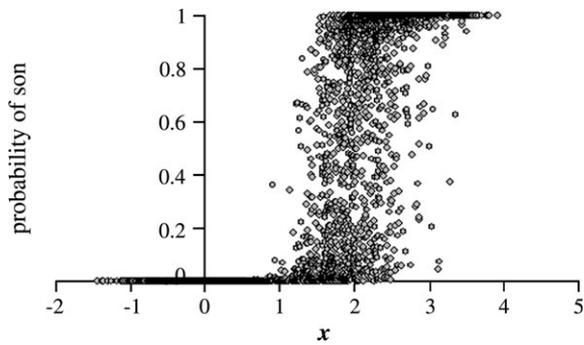


Figure 6

An example of the relationship between male attractiveness and offspring sex ratios, for a continuously variable, Fisherian male trait with biased sex ratios (Model 2) and a gradual form of sex ratio adjustment (traits α and β , explained in main text). The male's trait phenotype (x) and the probability of producing a son are shown for all mated pairs in the 50 000th generation of one simulation run. Each point represents a separate mating. Parameter values are given in the main text.

However, the change in the sex-allocation traits is not significant. Selection on these traits is evidently quite weak.

DISCUSSION

Our simulations confirm that sex ratio adjustment based on male attractiveness can evolve, such that females with attractive partners produce more sons than those with unattractive partners. However, it appears that the selection pressures responsible for this pattern are rather weak. This suggests that in many animal populations, we may be unlikely to detect any clear relationship between male attractiveness and the sex ratio.

Pattern of sex ratio adjustment

As predicted by quantitative genetic models (e.g., Iwasa et al. 1991; Pomiankowski et al. 1991), sexual selection can only maintain a costly male trait and a costly female preference in an exaggerated state, away from their survival optima, when the male trait is a Fisherian trait under mutation bias or a conditional (or revealing) indicator. In both of these scenarios, the same qualitative pattern of sex ratio adjustment subsequently evolves: females with attractive mates produce more sons than those with unattractive mates. This fits with widespread verbal arguments and makes good sense because sons inherit their father's attractiveness. The fact that the same pattern appears for both discrete and continuous variation in the male trait, in both Fisherian and good-genes models, and for both abrupt (bang–bang) and gradual sex ratio adjustment suggests that this result is widely applicable.

The quantitative pattern of sex allocation, however, depends on the type of model we use. For discrete variation (Model 1), where males either express the trait to its full extent or do not express it at all, the major sex ratio bias is seen in the offspring of unattractive males. Females with attractive, trait-bearing partners hardly deviate from a 50:50 sex ratio, whereas those with unattractive, traitless partners greatly overproduce daughters. This was predicted from an earlier model of evolutionarily stable sex-allocation strategies by Pen and Weissing (2000). Though at first sight it seems unrealistic to model the male phenotype as having only 2 possible states, some conspicuous traits may in fact fit this caricature well. Some striking plumage features in birds are governed by a small number of genes (Grant PR and Grant BR 1997; Theron et al. 2001), and work

on *Drosophila* has shown that genetic differences at a single locus can dramatically affect male attractiveness (e.g., Ringo et al. 1992; Singh and Sisodia 1999). It is possible, then, that a single mutation could create a novel male trait, dividing the male population into 2 distinct types: those that possess the novel trait and those that lack it. If females are more attracted to the novel phenotype, the trait will spread through sexual selection to most of the males. According to the results of our simulations, there should then be a selection pressure for females to overproduce daughters if they happen to end up with an unattractive, traitless partner.

Although this simple scenario of all-or-nothing expression may apply in certain cases, most sexually selected traits are likely to show a continuous range of expressed values (Andersson 1994; Grant PR and Grant BR 1997). In such cases, encapsulated by Model 2, we predict that offspring sex ratios should be biased not only by females with unattractive partners, who have more daughters, but also by those with attractive partners, who have more sons. Thus, the conclusion of Pen and Weissing (2000) that sex ratio biases should be largely restricted to females with unattractive partners seems to be a consequence of considering only 2 male types.

The grouping of males into 2 types also explains why, under the bang–bang form of adjustment (traits s_+ and s_-) in the Fisherian version of Model 2, the sex ratio bias for unattractive males is stronger than that for attractive males (Figure 4, middle). Due to their greater attractiveness, males with above-average trait expression are responsible for most of the matings, and the sex ratio bias is therefore tempered strongly by selection pressures favoring the rarer sex. Males with below-average expression are less well represented in the mating population, and so stronger sex ratio biases are possible. By categorizing males into 2 types according to their trait expression, the s_+ and s_- sex-allocation traits bear some similarity to the S_1 and S_0 loci of Model 1. For the gradual form of adjustment (traits α and β), in contrast, the degree of bias for females mated to the most attractive and the least attractive males is very similar (Figure 6). In answer to the question posed in the title of this paper, attractive males should indeed have more sons, just as unattractive males should have more daughters.

The clearest pattern of sex ratio adjustment was seen for a Fisherian trait subject to biased mutations (middle panels of Figures 1, 4, and 5), in which males varied in heritable attractiveness but not in heritable viability. In this situation, only sons inherit paternal attractiveness, which is why females mated to highly attractive partners are selected to produce a more male-biased offspring sex ratio than those with unattractive partners. In the good-genes version (conditional indicator), however, daughters as well as sons profit from having a father who is attractive because his attractiveness indicates high heritable viability for both sexes. It is perhaps not surprising, then, that under this scenario, sex ratio biases were less marked and showed inconsistency between simulation runs. In line with Burley (1986), we predict that strong biases are most likely to be seen in species where the heritable benefits of mating with an attractive male are largely sex limited.

Strength of selection on sex ratio adjustment

Although our results confirm that sex ratio adjustment with respect to male attractiveness can evolve, a consistent feature of our simulations is that this process takes a great deal of time. Only very slight sex ratio biases were seen after 5000 generations, and for all models, it took at least 40 000 generations for the full extent of the bias to emerge. For the conditional handicap in Model 2, the offspring sex ratios for attractive and unattractive males were barely different from 0.5 even after 50 000 generations of evolution.

It is important to point out here that the “generations” in our simulations have no direct correspondence to the generations of a real organism. To make such a link, we would need to know the precise details of the genetic system controlling the traits involved and have reliable estimates of the frequency and effects of mutations in these traits. Furthermore, our simplifying assumption of nonoverlapping generations does not hold for many real populations. For these reasons, we cannot say whether a pattern found after 50 000 generations of our simulation would appear more quickly or more slowly in a natural system.

Nonetheless, by comparing the evolution of sex ratio adjustment with that of the male trait and female preference, it is clear that selection on sex ratio adjustment is far weaker. The male trait reaches an exaggerated state within 500 generations, and often much sooner than that, whereas the sex-allocation traits show only slight changes after several thousand generations. This is not due to insufficient variation; new mutations occur just as often in the sex-allocation traits as in the male trait and female preference, and even with a mutation rate 4 times higher ($\mu_S = 0.2$), there is still very little sex ratio bias after 5000 generations (unpublished results). Overall, the slow rate of evolution implies that selection on sex ratio adjustment with respect to male attractiveness is weak. This probably reflects that, in general, selection on the variable part of a conditional trait (e.g., how the sex ratio varies with attractiveness) is weak compared with selection on the mean value of that trait (e.g., the mean sex ratio) or on a non-conditional trait. We should therefore not be surprised if, in natural populations, attractive male traits show little relationship with offspring sex ratio, particularly if those traits have evolved relatively recently.

Constraints on sex ratio adjustment

To investigate the adaptive basis of sex ratio adjustment, we omitted from our models many possible factors that might constrain the evolution of such strategies in real animals. First, through the evolution of the sex-allocation traits, we allowed females to have full control over the sex of their offspring, free from any mechanistic constraints or costs. In animals with chromosomal sex determination, it may be that Mendelian segregation of the sex chromosomes is not amenable to manipulation by parents (Williams 1979; Krackow 2002; though, for an alternative viewpoint, see West and Sheldon 2002 and West et al. 2005). Manipulation may be possible after meiosis, for example, in birds through the selective resorption, selective ovulation, or selective fertilization of Z- and W-bearing ova (Pike and Petrie 2003), but this is likely to entail some energetic costs, which were not included in our models. Costs of sex ratio control are expected to weaken any bias (Pen et al. 1999). In general, very little is known about how sex ratio biases might be achieved, and in the absence of clear evidence for a suitable mechanism, we must consider the possibility that such manipulation is beyond maternal control or too costly to be worthwhile.

Second, we assumed that females had perfect information about a male's genetic quality (whether in terms of heritable attractiveness or heritable viability). In real systems, however, there will always be some “noise” associated with both signaling and receiving; males will not advertise their quality perfectly accurately, and females will not perceive male phenotypes perfectly accurately. This error means that females will be uncertain about the true quality of their mate and therefore might be expected to hedge their bets somewhat by reducing the degree of any sex ratio bias (Charnov et al. 1981; but see Pen I, Lessells CM, Weissing FJ, and Colegrave N, in preparation). The upshot is that sex ratios might be less strongly biased than those pre-

dicted by our models. In support of this, uncertainty regarding the consequences of sex ratio adjustment seems to have such an effect in parasitic wasps (West and Sheldon 2002).

For the bang–bang form of sex allocation, we made a further assumption about the information available to females, namely, that they were aware of the average trait phenotype for all males in the population. We feel it is not unreasonable to assume that a female would have some estimate of this average through her mate-sampling behavior and encounters with males in other situations, but it is highly unlikely that she would know the true average value. For the same reasons discussed above, the error in her estimate might reduce the extent of sex ratio bias.

The aim of our models was to determine whether it makes sense, adaptively, for mothers to manipulate the sex of their offspring in relation to their partner's attractiveness. We have shown that there is indeed an adaptive reason for such manipulation when it is free from constraints or costs but that even in this unrealistically conducive situation it appears to be weak. What our models do not show is that this kind of manipulation will necessarily take place in nature. With constraints and costs acting against sex ratio adjustment, we expect patterns of bias to be even weaker than those found in our simulations.

Advantages of the simulation approach

The individual-based simulations we used in this study, though lacking some of the insight of analytical methods, have some important strengths. First, they clearly illustrate the dynamics of selection in a system where stochastic processes such as mutation and genetic drift are part and parcel of the evolutionary process. Second, in contrast to most quantitative genetic models, we do not need to assume particular values for the variances and covariances of the traits of interest but rather allow these to develop in response to selection. Third, and for the present study most crucially, it is sometimes possible to build simulation models for situations where an analytical approach is difficult and perhaps unfeasible. Taking the quantitative genetic model of Pomiankowski et al. (1991) as an example, it is not obvious how one would calculate the selection gradient for a conditional sex-allocation strategy in this framework. It is also unclear what kind of values, or even their signs, would be realistic for the genetic variances and covariances between the sex-allocation traits and the male trait and female preference. Finally, the quantitative genetic approach focuses on mean values, whereas for our research question, it is the variance in traits that is of central importance. A simulation study avoids all these problems by directly monitoring the genetic values for each individual in the population.

Possible extensions

Our models can easily be modified to take account of additional complications that might be present in some biological systems. For example, evidence suggests that many conspicuous male traits and female preferences in birds and butterflies are coded by genes located on the sex chromosomes and therefore show sex-linked inheritance (Reeve and Pfennig 2003; Kirkpatrick and Hall 2004). The models presented above assume autosomal inheritance of trait and preference, but we are currently investigating how patterns of sex ratio bias are affected by different kinds of sex linkage. Traits with sex-linked inheritance may often show sex-limited expression, in which case we would expect stronger selection for sex ratio adjustment. Similarly, Fisherian sexual selection is most pronounced when female preferences are Z-linked (Kirkpatrick and Hall 2004), and so we might expect to see greater sex ratio biases under this form of inheritance.

Another interesting complication is that some genes may have sexually antagonistic effects, in that they increase the fitness of one sex but decrease the fitness of the other (Chippindale et al. 2001). In the simulations presented above, the genes coding for male trait expression may enhance the direct fitness of sons (via increased attractiveness), but they are neutral with respect to the direct fitness of daughters (who do not express the trait). We could alter this situation by reducing the survival of daughters carrying genes for strong trait expression. This would magnify the difference in fitness returns from sons and daughters for females mated to highly ornamented males and is therefore likely to strengthen the degree of sex ratio bias.

Concluding remark

Overall, we can confirm the intuition that attractive males should have more sons, but we argue that selection on this is weak and may be counteracted by constraints and costs of manipulation. Viewed in this light, the mixed evidence for adaptive sex allocation in birds (Clutton-Brock 1986; Sheldon 1998; Komdeur and Pen 2002; Krackow 2002; West and Sheldon 2002; West et al. 2002; Ewen et al. 2004; Cassey et al. forthcoming) is not so surprising.

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