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THE COMPLEX INTERPLAY OF SEX ALLOCATION AND SEXUAL SELECTION

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It is well recognized that sex allocation strategies can be influenced by sexual selection, when females adjust offspring sex ratios in response to their mates' attractiveness. Yet the reciprocal influence of strategic sex allocation on processes of sexual selection has only recently been revealed. Recent theoretical work demonstrates that sex allocation weakens selection for female preferences, leading to the decline of male traits. However, these results have been derived assuming that females have perfect knowledge of mate attractiveness and precise control over cost-free allocation. Relaxing these assumptions highlights the importance of another feedback: that adaptive sex allocation must become difficult to maintain as traits and preferences decline. When sex allocation strategies erode not only traits and preferences but also their own selective advantage, predictions can no longer be expressed as a simple linear correlation between ornament exaggeration and adaptive sex allocation. Instead, strongest sex ratio biases may be found at intermediate trait levels.

KEY WORDS: Coevolution, eco-evolutionary feedback, female preference, ornament, perceptual constraint, primary sex ratio.

Extravagant male ornamentation is conspicuous in the animal world. The coevolution of ornaments and female preferences for ornamented males is central to the study of sexual selection, and has been a major focus of the field since its inception (Andersson 1994). Perhaps less aesthetically striking, but equally conceptually engrossing, the allied theory of sex allocation has generated a wealth of research on the factors influencing optimal investment into male and female function (i.e., offspring sex ratios; West 2009). Sexual selection and sex allocation are brought together through the recognition that females mated to attractive males benefit by overproducing sons, who will inherit their fathers' sexy traits (Burley 1981). When females choose their mates on the basis of ornamental traits, selection can exaggerate both the trait in question and the preference for it (review: Kokko et al. 2006). A central part of the benefit females gain by mating with the most attractive males is that attractive males father attractive sons (Taylor et al. 2007; Firman 2011; Prokop et al. 2012). Under such sex-limitation in the heritable benefits of ornaments, females paired to attractive partners capitalize on this advantage if they can produce mostly sons (Burley 1981, 1986; Fawcett et al. 2007; Cox and Calsbeek 2010), especially if daughters of attractive males have reduced fitness (review: Rice and Chippindale 2001). Similarly, females paired to less attractive partners can make the best of a bad job by producing daughters.

Considering sexual selection and sex allocation together as a jointly evolving system reveals previously unappreciated dynamics. In particular, it becomes apparent that conditional sex allocation is more than a mere product of selection: it can feed back into the selective environment for other traits. Recently, Fawcett et al. (2011) demonstrated that sex allocation in response to male attractiveness erodes selection on (and expression of) both the preferred male trait and the female preference (see also Pen and

Weissing 2000; Fawcett et al. 2007). Females effectively compensate for suboptimal mate choice by adjusting offspring sex ratios, reducing the fitness difference between females mated to different males. In turn, this reduces the fitness benefits of having a preference. In Fawcett et al. (2011)'s model, this ultimately led to the loss of male traits and associated preferences when sex ratio strategies were unconstrained. From this result they predicted that, all else being equal, the most elaborate sexual displays should be seen in species with little or no control over offspring sex.

The study of Fawcett et al. (2011) is insightful in that it highlights the importance of feedbacks between two research fields whose links have been underexplored. Here we show that it also sets the stage for considering another feedback that is extremely likely to operate when traits of ornamented males diminish: selection for, and the ability to produce, a sex ratio bias must also decline. This additional feedback is prevented in Fawcett et al. (2011) by two assumptions: first, that the precision of sex ratio adjustment by mothers is perfect for any population-wide degree of male ornamentation, which requires that once mated, females possess perfect knowledge of the quality of their mate. Second, as conditional sex allocation has no cost, it persists even when ornamentation and preference are zero and there is no longer selection for the bias, because the individual strategy is neutral when the adult sex ratio is at equilibrium (Charnov 1982).

It appears important to relax these assumptions for several reasons. The degree of precision in conditional sex allocation differs dramatically between theoretical predictions and empirical data (West et al. 2002). Where theoretical approaches tend to predict sharp transitions in sex ratio across condition unless constraints on sex ratio bias or imperfect knowledge of condition are introduced (Pen et al. 1999; van Dooren and Leimar 2003; Schwanz and Proulx 2008), empirical data show much more gradual transitions in sex ratio bias (e.g., West et al. 2002). Smaller traits are likely to make it harder for females to distinguish between degrees of ornamentation, which will constrain the precision of sex allocation (West et al. 2002; West and Sheldon 2002). Comparison among species reveals that knowledge of condition dramatically influences the precision of the sex ratio bias (West and Sheldon 2002). There is likely to be a limit to the accuracy of perception: it is unrealistic to assume that arbitrarily small differences between males can maintain a strong response in females, and perceptual constraints will instead play a role.

In addition, the benefit to producing sons when mated to ornamented males necessarily declines when the male trait and female preference decrease, such that the sex allocation strategy is unlikely to persist in the absence of selection for it if its expression is costly. Under some mechanisms of sex ratio manipulation, steeper response curves (which ensure good ability to differentiate between mate types that select for different sex ratios) may be costlier to achieve: a steep curve predicts that offspring of the "wrong" sex are almost never produced. If this requires, say, selective abortion, the associated fecundity or time costs can have a significant impact on the evolving strategies (Pen et al. 1999; Pen and Weissing 2002).

By presenting a model that relaxes key assumptions of Fawcett et al. (2011), we show that sexual selection may stabilize, rather than fully erode, when sex ratio biases can evolve: sex ratio responses diminish traits but the coevolutionary feedback can halt this process before traits vanish.

Methods

We expand on the individual-based simulation presented in Fawcett et al. (2011) to include the ideas that (1) females are unlikely to be able to detect small differences in male trait value, thus will likely produce similar sex ratio biases when mated to males with similar trait exaggeration and (2) costs associated with extreme sex ratio biases mean such biases are unlikely to be maintained if selection is absent.

Our simulated populations contain 5000 individuals described by genetic trait values for four traits, assumed to be diploid and autosomal with no linkage and no dominant gene action. The first two traits, male ornamentation (t, expressed only in males) and female preference for male ornamentation (p, expressed only in females) are modeled as in Fawcett et al. (2011). The remaining two, denoted α and t_{piv}, describe the sex ratio response of a female to her mate's trait t, and are expressed only in females. Rather than using a two-state response, we assumed that the probability an offspring is male is determined as

$$\Pr(\text{male}) = \frac{1}{1 + \exp(-\alpha[t - t_{\mathrm{piv}}])}. \tag{1}$$

The larger the value of α, the more step function-like a female's response, and $\alpha = 0$ predicts no sex ratio response such that $\Pr(\text{male}) = 0.5$ regardless of the male's traits. The value of the inflection point t_{piv} indicates which male trait value t makes a female produce a 50:50 sex ratio. Note that a mismatch between t_{piv} and the distribution of t in the population can make sex ratio biases costly in an indirect manner, in addition to the direct cost described later. If females use, say, $t_{\mathrm{piv}} = 1$, and most males have $t > 1$ (or < 1), then females as a whole overproduce males (or females), and pay the cost of producing the common sex (Schwanz et al. 2010).

The genetic values that determine male ornamentation and the sex ratio response were constrained to be positive, whereas female preference could be any real number. As in Fawcett et al. (2011), expression of male trait and female preference are costly, with a male's and a female's survival from birth to maturation equal to $\exp(-c_{\mathrm{m}}t^2)$ and $\exp(-c_{\mathrm{f}}p^2)$, respectively; here c_{m} and c_{f} are positive constants. A female's survival is additionally multiplied by exp($-c_\alpha\alpha^2$), where c_α is a positive constant, to implement our assumption that steep sex ratio responses can have direct costs. Individuals survive to maturity or are removed from the population (i.e., do not enter the mating pool) based on the combined survival probability given by genetic trait values (values for p and α for females and t for males).

Each generation, 5000 new offspring replace the previous generation (i.e., all adults die after reproduction). Each offspring is first assigned randomly to a living female who becomes the mother. Ten living males are then randomly selected as the set available for the mother to choose from, and the probability that each of them is the sire is proportional to their attractiveness exp($-c_p pt$), where c_p is a positive constant (see Fawcett et al. 2011), p is the mean of the female's two alleles for preference, and t is the mean of the male's two alleles for the sexually selected trait. Offspring genotype for all four traits is determined by Mendelian inheritance (one randomly chosen allele from the mother, one from the father). Mutation occurs in a fraction of offspring, independently across all alleles (μ_p for preference, μ_t for male ornamentation, μ_s for sex-ratio slope, and μ_{piv} for the pivotal trait value). For female preference, new genetic values in mutants increase or decrease from the original value in equal likelihood by an amount drawn from a uniform probability distribution of width 0.5. Mutation in male ornamentation genetics and in sex ratio response traits occurs similarly, except that allelic values have a lower bound of zero, and for the male trait the mutant genetic value also decreases by g (such that the change in trait genotype is found in the range [$-0.25-g$, $0.25-g$]).

We created a dataset of 125 cases that were each run for 5000 generations (see Results and figure legends for parameter details). All female preference alleles were initialized at $p = 1$ and male traits at $t = 0$ as in Fawcett et al. (2011); we additionally initialized all sex ratio alleles of all individuals as $\alpha = t_{piv} = 0$. Variation was then introduced through mutations as described earlier, but for the sex ratio traits the mutation rate was set to zero for the first 500 generations. Evolution of the sex ratio strategy thus began at generation 500. In rare cases (mostly when female preference was very cheap), we observed extinctions, preceded by a total lack of one sex. Extinct populations were replaced by returning the population to its starting condition and rerunning all 5000 generations.

We quantify the evolved strength of a response at generation 5000 (or any other generation) in the following way. Each female is hypothetically mated with every male present in the population, and the consequent absolute value of the difference to the neutral sex ratio 0.5 is noted. The female's mean sex ratio response is the average of all these responses, weighted by the probability of this mating actually occurring: the weight is proportional to the male's attractiveness to her, exp($-c_p pt$). This value is the expected value of the bias (from 1:1 ratio) that an empiricist would see in offspring resulting from actual matings. In a simplified example, imagine a population consisting of only one female and two males. The female has a 90% probability of mating with male A, with whom she produces a sex ratio of 0.7, and a 10% probability of mating with male B, in which case she produces a sex ratio of 0.45. The strength of her sex ratio response has the expected value $0.9 \times 0.2 + 0.1 \times 0.05 = 0.185$. The mean of this value across all females is the strength of the sex ratio response in the entire population. If all females use sex ratio 0.5 regardless of mate attractiveness, the value is 0. In all other cases, the value is positive.

Results and Discussion

To examine the evolutionary dynamics of the system across wide parameter space, we simulated 15 different cases for the sex ratio bias cost c_α, additionally choosing five different values for the female preference cost c_f. High costs of a sex ratio response should limit the degree to which it evolves, so we might predict a weaker sex ratio response and greater maintenance of the male trait under high cost. To contrast the outcomes in these cases to the baseline expectation when females lack the ability to bias sex ratios, we ran an additional 10 replicate simulations, without allowing sex ratio responses to evolve, for each of the five female preference cost values c_f. We depict the outcomes as a mosaic (Fig. 1), with the size of the circle corresponding to ornament size, and the shade of the background indicating the strength of the sex ratio response as measured at generation 5000. An obvious interpretation of the overall mosaic is that we have created a hypothetical dataset of 125 species, of which many can bias sex ratios and many others cannot—either because there is no sex ratio biasing mechanism present (50 species) or because the cost of biasing might be prohibitively high (some of the 75 remaining species).

Across all simulated cases, traits and female preferences covary extremely well (Spearman rank correlation $r_S = 0.992$, $n = 125$, $P < 0.0001$), thus the coevolution (including co-collapse) of traits and preferences follows standard sexual selection theory. High stochasticity in the outcomes reflects that the system never converges in the usual sense, and a finite population instead experiences continual change in the strength of mate preferences. Overall patterns are therefore more reliably measured by comparing a large number of species after a substantial number of generations than by examining idiosyncratic features of any particular simulation run.

The model by Fawcett et al. leads to the expectation that the strongest sex ratio responses (darkest shades in Fig. 1) would be found where ornaments are smallest (smallest circles in Fig. 1). Instead, a pattern emerges where ornaments can disappear from the population both (A) deterministically where female preference

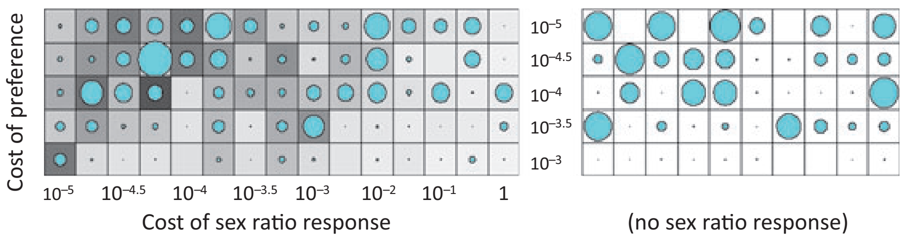

Figure 1. The simulated dataset of 125 species, arranged such that each row uses a specific cost of female prefence ($c_{\mathrm{f},}$ logarithmically spaced between 10^{-5} and 10^{-3}) and each column uses a specific cost of sex ratio response c_α (logarithmically interpolated, such that the value used between $c_\alpha = 10^{-5}$ and $10^{-4.5}$ is $c_\alpha = 10^{-4.75}$) or, on the right side where sex ratio responses are prevented from occurring (making c_α irrelevant), the columns indicate different replicates. The radius of the circle is proportional to male trait t at generation 5000, the dark shading is proportional to the strength of the sex ratio response (see Methods for definition). Other parameters: $c_\mathrm{m} = 0.5$, $c_\mathrm{p} = 1.0$, $\mu_\mathrm{p} = \mu_\mathrm{t} = \mu_\mathrm{s} = \mu_\mathrm{piv} = 0.05$, and $g = 0.02$.

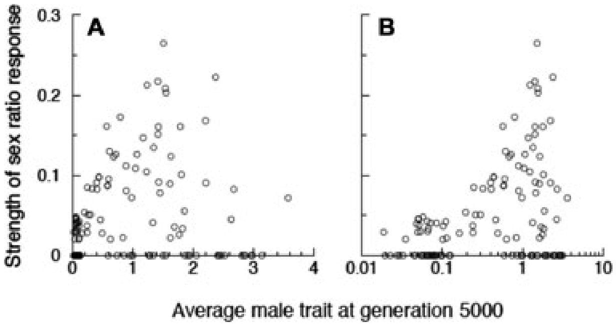

Figure 2. The largest male traits do not occur with the strongest sex ratio responses (A), however as a whole, the relationship is positive (B). Note the bimodal distribution of the male trait in the absence of any sex ratio response (values along the x-axis, most apparent in the log-scaled plot (B).

costs are high (whether or not sex ratio responses are in principle allowed to evolve), and (B) stochastically throughout the simulated range of parameter values (again, whether or not sex ratio responses are allowed to evolve). In both (A) and (B), the sex ratio responses are weak in cases where ornaments have disappeared: the shades tend to be lighter when circles are small (Fig. 1). Strong sex ratio responses (dark shades) instead tend to occur where ornaments are modestly developed, rather than minimal. These appear to co-occur with low costs of sex ratio responses, as well as low costs of female preferences (Fig. 1: shades are darkest near the top left).

If an empiricist were to analyze such a dataset, a simple linear regression of the raw values (Fig. 2A) would show a significant, positive association between sex ratio response and male trait ($r^2 = 0.03$; $F_{1,123} = 4.16$, $P = 0.04$; although heteroscedasticity of the data would have to be considered). This contrasts with a prediction that is tempting to infer from Fawcett et al. (2011), that the two be negatively correlated across species. Nevertheless, in light of our simulation a positive relationship is not incompatible with their central idea that sex ratio responses erode traits and preferences. If we want to know whether responses tend to diminish male traits from the extremes they can reach when sex ratios do not vary, the question to ask about the dataset becomes a more specific one: are the largest trait values disproportionately often found where sex ratio biases are too costly to evolve or are prevented from evolving at all? Although this appears to be the case, the complex pattern of Fig. 1 prevents the matter from being settled by simple visual inspection.

Figure 2A provides support for the erosive nature of sex ratio strategies in the "humped" nature of the data: the strongest male *trait* values are found when sex ratio responses are small, or prevented from evolving and hence zero (species forming the low right of the hump). The strongest *sex ratio responses*, in turn, are associated with male traits that are intermediate on a linear scale. Small male traits are only associated with weak sex ratio responses (species forming the low left of the hump), which supports the notion that sex ratio responses cannot be maintained if large trait values are eroded or never evolved in the first place. A log-scale plot (Fig. 2B) makes it clearer that when sex ratio responses cannot occur at all (all such species are along the x-axis), the outcome is strongly bimodal: the trait virtually disappears or is maintained at a strong level.

When we consider that male traits can disappear stochastically, for reasons that have not necessarily much to do with sex ratio responses, testing the hypothesis that sex ratio responses diminish otherwise persistent traits but the coevolutionary feedback can halt this process before traits vanish requires us to ask whether ornaments are disproportionately often maintained at an *intermediate* level when sex ratio responses exist. Thus, the effect of sex ratio strategies on the evolution of male ornaments can be simultaneously erosive and stabilizing.

We can test for these two effects of sex ratio strategies (erosion of traits, and their subsequent stabilization instead of disappearance) by examining how many cases (i.e., species) have intermediate trait values across the range of sex ratio strategies. The dataset splits itself into 3 roughly equally sized portions when traits < 0.1 are defined as "small" (37 spp), those > 1 are "large"

Table 1. Two alternative classifications of cases: whether the underlying cost structure is known (rows 1–3) or not (rows 4–6), there is a nonrandom association between the rows and columns. Importantly, in all methods of analysis, the complete absence of species that combine strong sex ratio responses with a lack of male traits shows that species exhibiting small ornamental trait values cannot maintain strong strategic sex allocation. Similarly, strategic sex allocation is most likely in species with the most extreme and exaggerated ornamentation, which provide the strong selective environment promoting the evolution of conditional strategies.

	Trait < 0.1	Trait > 0.1 but < 1	Trait > 1	Total
no sr allowed	23	8	19	50
sr cost $\geq 10^{-3}$	8	15	12	35
sr cost $< 10^{-3}$	6	16	18	40
sr response < 0.05	37	19	25	81
sr response > 0.05 but < 0.1	0	14	7	21
sr response > 0.1	0	6	17	23
Total for each	37	39	49	125

(49 spp), and in between traits are "intermediate" (39 spp). Similarly, with perfect knowledge of the underlying costs, we can divide species into categories "no sex ratio responses allowed" (50 species), "allowed but costs are high" (35 species when defining 10^{-3} as the threshold cost), and "allowed and costs are low" (40 species when defining 10^{-3} as the threshold cost; Table 1). The distribution of species across these categories significantly differs from random ($\chi^2 = 15.3$, $P = 0.004$). In particular, intermediate values of male traits are underrepresented when the sex ratio response cannot evolve. Thus, allowing a sex ratio response does lead to more traits being maintained at intermediate values. Interestingly, the increase in intermediate male trait values is due to a reduction in the number of low-trait cases and not a decrease in cases with high trait values. Thus, although the evolution of a sex ratio response may erode male ornaments and female preferences, its more obvious effect is to stabilize the coevolution of these traits at a point where coevolutionary erosion of traits, preferences and sex allocation comes to a halt.

Empirically testing this prediction becomes complicated when we consider that we are unlikely to know with certainty a species' ability to bias sex ratio or the associated costs. A researcher faced with a real empirical dataset resembling that generated by our simulation is less likely to detect sex ratio responses less than 0.05 than greater biases. To reflect this, we can group the species into three trait categories as above, but now use three empirically estimated sex ratio categories: "response absent or too small to be detected unless sample sizes are large, < 0.05" (81 species), "more likely to be detected but effect size remains small, ≥ 0.05 but < 0.1" (21 species), and "large and likely to be detected, ≥ 0.1" (23 species; Table 1). The distribution of the data is, again, significantly different from random ($\chi^2 = 47.7$, $P < 0.0001$). This grouping reveals the outcome that strong sex ratio responses do not co-occur with small trait values and are instead associated with larger trait values. This grouping also reveals that just over half (25 of 49) of all the cases where the trait value is categorized as "high" are associated with a very weak sex ratio response, presumably because in these cases a sex ratio response was not allowed at all or was very costly. In this hypothetical empirical dataset, the erosive and stabilizing effects of sex ratio response are only partially evident in the overabundance of extreme trait values when there is no sex ratio response and the lack of small trait values when sex ratio responses are detectable.

Thus, as soon as one relaxes the assumptions that females have perfect knowledge of male quality and that sex ratio strategies can persist without cost in the absence of selection for them, the erosion identified by Fawcett et al. (2011) will not straightforwardly translate into a negative relationship. It is important to realize that impact of a continuing feedback loop between trait and sex ratio response: not only does strategic sex allocation diminish male traits, but diminishing male traits weaken sex ratio responses. Testing the prediction that sex ratio response erodes male trait exaggeration is rather daunting. Even if we could measure sex ratio control and compare the extent of ornamentation across species, the complex dynamics of a large number of contributing factors will make it difficult to derive directional predictions and/or empirically tease apart the importance of different effects. Multiple interacting mechanisms can prevent trait evolution: preference costs may be too high, or if they are sufficiently low, sex ratio responses may erode the trait and the preference, provided sex ratio responses are not themselves too costly. An experimental evolution approach might under such conditions provide greater insight. Do the ornaments we see have the potential to be more exaggerated were they not eroded by sex allocation? If even sex ratios were artificially imposed on females of a strategically allocating species, would the level of male ornamentation increase over evolutionary time?

Considering the incidence of collapse in male trait and female preference coevolution highlighted an unanticipated but important implication of sex allocation for the evolution of male ornaments. In our simulations, small male traits were less common when a sex ratio response was allowed (Table 1), suggesting that females' ability to bias the sex ratio stabilizes the sexual selection system. This may reflect trait-preference evolution becoming "too exaggerated" in the absence of sex ratio response and subsequently undergoing a collapse (see also Iwasa and Pomiankowski 1995). Strategic sex allocation may moderate this process, preventing male traits from becoming extremely exaggerated and the sexual selection system from collapsing.

Despite their complicated nature, the implications of Fawcett et al. (2011) and our model remain dramatic, and should compel behavioural ecologists to consider other scenarios where sex allocation may produce evolutionary feedbacks. For example, does sex allocation in cooperative breeders influence group size and alter selection on sociality? Does sex allocation in response to genetic incompatibility of mates reduce selection for female preferences, given that variation in incompatibility must persist for preferences to be maintained? More broadly, given naturally observed patterns of ornamentation, this new information may improve our understanding of the comparative effects of sexual selection and offspring sex allocation. Perhaps taxa with a tendency to evolve strongly exaggerated ornaments tend to lack mechanisms to substantially bias offspring sex ratios. Limits to sex ratio bias have been suggested to reflect physiological constraints on maternal manipulation, weak selection on sex allocation (Fawcett et al. 2007; Cockburn et al. 2002) or both. Building on the insights of Fawcett et al. (2011), our model offers another potential constraint on the extent of sex ratio bias: sex allocation strategies erode their own selective advantage through their effects on traits and preferences.

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