

Sexual Selection Favors Female-Biased Sex Ratios: The Balance between the Opposing Forces of Sex-Ratio Selection and Sexual Selection

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ABSTRACT: In a verbal model, Trivers and Willard proposed that, whenever there is sexual selection among males, natural selection should favor mothers that produce sons when in good condition but daughters when in poor condition. The predictions of this model have been the subject of recent debate. We present an explicit population genetic model for the evolution of a maternal-effect gene that biases offspring sex ratio. We show that, like local mate competition, sexual selection favors female-biased sex ratios whenever maternal condition affects the reproductive competitive ability of sons. However, Fisherian sex-ratio selection, which favors a balanced sex ratio, is an opposing force. We show that the evolution of maternal sex-ratio biasing by these opposing selection forces requires a positive covariance across environments between the sex-ratio bias toward sons (b) and the mating success of sons (r). This covariance alone is not a sufficient condition for the evolution of maternal sex-ratio biasing; it must be sufficiently positive to outweigh the opposing sex-ratio selection. To identify the necessary and sufficient conditions, we partition total evolutionary change into three components: (1) maternal sex-ratio bias, (2) sexual selection on sons, and (3) sex-ratio selection. Because the magnitude of the first component asymmetrically affects the strength of the second, biasing broods toward females in a poor environment evolves faster than the same degree of bias toward males in a good environment. Consequently, female-biased sex ratios, rather than male-biased sex ratios, are more likely to evolve. We discuss our findings in the context of the primary sex-ratio biases observed in strongly sexually selected species and indicate how this perspective can assist the experimental study of sex ratio evolution.

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When the cost of producing a male equals the cost of producing a female, natural selection acting on autosomal genes favors an equal sex ratio (Fisher 1930; Frank 1983). This observation appears in most textbooks on evolution (e.g., Freeman and Herron 1998, p. 624; Futuyma 1998, pp. 613–616; Ridley 1998, pp. 294–300) and behavior (Krebs and Davies 1991, p. 254; Drickamer et al. 2002, p. 306) as well as in most discussions of evolution in sexual species (e.g., Low 2000, p. 104). It is arguably more familiar to biologists than R. A. Fisher's many other contributions to genetics.

Fisher's sex ratio theory is most commonly formulated in terms of energetic investment in male and female offspring by female parents. Fisher suggested that members of the majority sex were energetically "cheaper" and parental investment theory has been developed along these lines (Trivers 1972; Clutton-Brock et al. 1984; but see Shuster and Wade 2003). This theory suggests that under certain circumstances, females may manipulate brood sex ratios by differential investment in offspring of a particular sex. Linking this reasoning to sexual selection, Trivers and Willard (1973) proposed a verbal model in which selection favors mothers that produce sons when in good condition but daughters when in poor condition (Cameron and Linklater 2000, 2002; Carranza 2002). Trivers and Willard (1973) reasoned that if maternal condition affects outcome of the reproductive competition experienced by a mother's sons, then the sons of a mother in poor condition will lose in contests with sons of mothers in good condition. In the words of Carranza (2002, p. F1), interpreting Trivers and Willard (1973), "male fitness will gain comparatively more than female fitness by slight advantages in condition." Consequently, mothers in poor condition should produce more daughters or invest more parental effort in daughters rather than squander investment of reproductive resources on sons destined to be losers in reproductive

competition with other males. Conversely, mothers in good condition should produce more sons or expend more effort on sons.

Bull and Charnov (1988, 1989; see also Bull 1981; Charnov and Bull 1989*a*, 1989*b*) provided similar but more quantitative analyses of investment in brood sex ratio in the context of environmental sex determination (ESD). They predicted that maternal selection favors brood sex ratios biased toward the sex produced in the poorer environment: “The population primary sex ratio ... may deviate substantially from 1/2 at equilibrium ... [and] should favor the sex that is overproduced in the patches of poorer quality” (Bull and Charnov 1988, p. 107). When sex differences in relative fitness occur in the absence of maternal control of sex, the predicted sex ratio is governed by Fisherian sex-ratio selection and is expected to evolve toward one-to-one (Shaw and Mohler 1953). When sex is determined environmentally, however, the equilibrium primary sex ratio is biased toward the sex produced in those environments that result in lower fertility or fecundity (Bull 1981; Bull and Charnov 1988, 1989; Frank and Swingland 1988; Charnov and Bull 1989*a*, 1989*b*; Freedberg and Wade 2003, in press).

Although unbiased sex ratios are predicted to predominate in nature, there are many known exceptions (Hamilton 1967), particularly in species with local mate competition (Frank 1990, 1998, p. 191–213), haplo-diploid genetic systems, maternally inherited microbes, meiotic drive, or conspicuous sex dimorphisms. The latter category is growing with a number of recent reports of facultative alteration of sex ratio in sexually selected species (Atlan et al. 1997; Komdeur et al. 1997; Whiteman 1997; Hurst and Pomiankowski 1998; Partridge and Hurst 1998; Wilkinson et al. 1998; Whittingham and Dunn 2000; Freedberg and Wade 2003; see also “Discussion”).

Recent discussions of maternal influences on brood sex ratio (Cameron and Linklater 2002; Carranza 2002) have questioned the specific predictions of the Trivers and Willard (1973) hypothesis (hereafter referred to as the TW hypothesis) and debated the empirical observations that would constitute confirmation or refutation of the TW hypothesis. Some authors have called for a “greater integration of empirical and theoretical work on the TW hypothesis” (Carranza 2002, p. F3; see also Clutton-Brock 1991). However, others have suggested that the simplicity and extendability of the TW model is powerful because it can be applied “to almost any situation in which an environmental variable has differential effects on the value of male and female offspring” (Sheldon and West 2002, p. 1043). These authors conclude, “In some cases where data do not fit theoretical predictions, it may be that this represents a failure by the researcher to understand the biology of the system rather than a failure of the theory.”

In this article, we present an explicit population genetic model wherein mothers of some genotypes facultatively alter brood sex ratio (primary sex ratio) in response to environmental conditions. Also in our model, the sons of mothers in good condition are better reproductive competitors than the sons of mothers in poor condition. We do not assume a sex difference in maternal investment in sons and daughters other than the numerical one, so our theory is not a completely general investigation of the TW hypothesis. However, equal maternal investment in both sexes (as in our model) generates the strongest selection for a balanced sex ratio, which opposes selection for maternal sex-ratio biasing. Thus, if a maternal allele for altered brood sex ratio can invade with equal investment, it suggests that it would also invade with unequal investment, particularly with excess investment in the minority sex. We determine the theoretical conditions necessary for the evolutionary pressure toward female-biased sex ratios to exceed the ubiquitous and opposing sex-ratio selection toward a balanced sex ratio. It is important to remember that any maternal gene that biases the sex ratio becomes overrepresented in the majority sex and is thus opposed by sex-ratio selection, which favors the minority sex. We derive an explicit, quantitative formulation for the sexual selection component of the TW hypothesis (eq. [18b]). Our formulation shows clearly that a positive covariance between brood sex-ratio bias and male reproductive success is necessary for the TW hypothesis. However, this covariance alone is insufficient to govern the evolutionary dynamic.

The Model

Let e_1 be the frequency of the poor environment, E_1 , and e_2 be the frequency of the good environment, E_2 , so that

Table 1: Maternal brood sex ratio conditional on the quality of the environment and on maternal genotype

Maternal genotype	Maternal environment	Fraction sons	Fraction daughters
B_1B_1 :	E_1	.5 + $2b_1$.5 - $2b_1$
	E_2	.5 + $2b_2$.5 - $2b_2$
B_1B_0 :	E_1	.5 + $1b_1$.5 - $1b_1$
	E_2	.5 + $1b_2$.5 - $1b_2$
B_0B_0 :	E_1	.5	.5
	E_2	.5	.5

Note: E_1 = poor environment; E_2 = good environment. Note that the values of b_1 and b_2 must be within the bounds $-0.25 < b_1, b_2 < +0.25$.

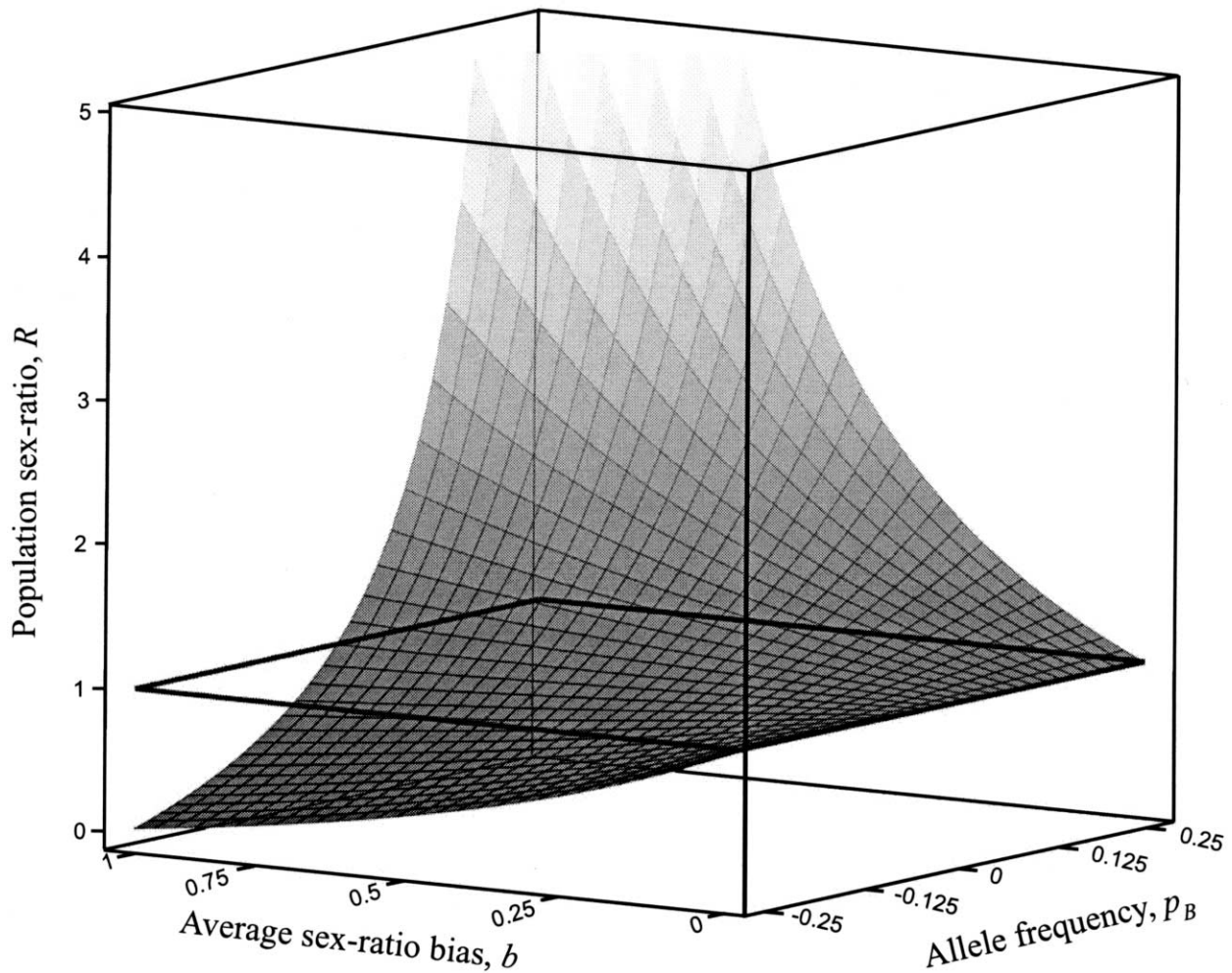


Figure 1: The effects of B_1 allele frequency, p , and average bias, b , on the primary sex ratio, R , expressed as the ratio $f_{\text{females}}/f_{\text{males}}$. Note that the effects on R of biasing toward females ($b < 0$) and biasing toward males ($b > 0$) are asymmetrical. It is this asymmetry that differentially affects subsequent sexual selection.

the sum, $e_1 + e_2$, equals 1. We assume that females experience the two environments randomly, in proportion to the occurrence of each. We postulate an additively acting, diploid, autosomal, maternal effect, sex-ratio biasing locus with alternative alleles, B_1 and B_0 . When mothers with genotype B_1B_1 experience a poor environment, they bias brood sex ratio toward sons by an amount $2b_1$. When they experience the good environment, they bias brood sex ratio toward sons by an amount, $2b_2$. The sex ratio biases in the broods of B_1B_0 mothers are b_1 in E_1 and b_2 in E_2 , respectively, while mothers, homozygous for the nonbiasing allele, B_0 , produce broods with equal numbers of sons and daughters. Thus, the action of the B_1 with respect to bias is additive.

The brood sex ratio biases, b_1 and b_2 , can be either

positive, meaning an excess of sons, or negative, meaning an excess of daughters. When E_1 is the poor environment, then, according to the TW hypothesis, it is adaptive for mothers to bias brood sex ratio so that $b_1 < 0 < b_2$. In the remainder of this article, we will assume that $b_1 < 0 < b_2$. That is, mothers in poor condition (in environment E_1) bias brood sex ratio toward daughters and away from sons. Conversely, mothers in good condition bias brood sex ratio toward sons and away from daughters. The brood sex ratios for all three maternal genotypes in each environment are given in table 1. Note that the values of b_1 and b_2 must lie within the bounds $-0.25 < b_1, b_2 < +0.25$. The average brood sex ratio bias of B_1B_1 mothers is $2(e_1b_1 + e_2b_2)$, while that of B_1B_0 mothers is $e_1b_1 + e_2b_2$. Since $b_1 < 0 < b_2$, the average bias, b , is positive when $e_1b_1 < e_2b_2$. B_0B_0 mothers

are incapable of altering brood sex ratio and produce equal numbers of sons and daughters in both environments (cf. table 1).

We define the mating success of males reared in environment E_1 as r_1 and that of males reared in environment E_2 as r_2 . We assume that the environment does not affect mean female fitness, W_{female} , measured in offspring numbers, but rather that a proportion of sons, $1 - r_1$, from the poor environment fail to mate and a proportion of sons, $1 - r_2$, from the good environment also fail to mate. Because E_1 is the poor environment, it means that $r_1 < r_2$. Thus, the average mating success, r , of a son of a B_0B_0 mother is $e_1r_1 + e_2r_2$. In contrast, the sons of mothers of the other two genotypes will enjoy greater mating success because more of them will be produced in the good environment than in the poor environment.

Let the frequency of B_1B_1 mothers be G_{11} , the frequency of B_1B_0 mothers be G_{10} , and that of B_0B_0 mothers be G_{00} , where the sum $G_{11} + G_{10} + G_{00} = 1$. The frequency of the B_1 allele in mothers, p , is $G_{11} + 0.5G_{10}$, and the frequency of the B_0 allele is q or $1 - p$. With these assumptions, the frequency of males in the population at birth, f_{males} , is

$$\begin{aligned} f_{\text{males}} &= G_{11}[e_1(0.5 + 2b_1) + e_2(0.5 + 2b_2)] \\ &\quad + G_{10}[e_1(0.5 + 1b_1) + e_2(0.5 + 1b_2)] \\ &\quad + G_{00}[e_1(0.5) + e_2(0.5)], \end{aligned} \quad (1a)$$

$$\begin{aligned} f_{\text{males}} &= 0.5 + 2pb \\ &= 0.5(1 + 4pb). \end{aligned} \quad (1b)$$

Similarly, the frequency of females at birth, f_{females} , is

$$\begin{aligned} f_{\text{females}} &= G_{11}[e_1(0.5 - 2b_1) + e_2(0.5 - 2b_2)] \\ &\quad + G_{10}[e_1(0.5 - 1b_1) + e_2(0.5 - 1b_2)] \\ &\quad + G_{00}[e_1(0.5) + e_2(0.5)], \end{aligned} \quad (2a)$$

$$\begin{aligned} f_{\text{females}} &= 0.5 - 2pb \\ &= 0.5(1 - 4pb). \end{aligned} \quad (2b)$$

Note that f_{males} and f_{females} always sum to 1. In addition, note that the upper limit to the average bias, b , of 0.25 insures that $0.0 < f_{\text{males}}, f_{\text{females}} < 1.0$. The ratio $f_{\text{females}}/f_{\text{males}}$ is R , the brood sex ratio at birth:

$$R = \frac{1 - 4pb}{1 + 4pb}. \quad (3)$$

The effects of the average bias, b , and the gene frequency, p , on R are shown in figure 1. The sex ratio, R , is female biased (i.e., $R > 1$) whenever $p > 0$ and $b < 0$ because of

the excess production of daughters in E_1 and the underproduction of daughters in E_2 by B_1B_1 and B_1B_0 mothers. Conversely, the brood sex ratio is male biased (i.e., $R < 1$) when p and b are > 0 . This occurs when the overproduction of sons in the good environment, E_2 , exceeds the overproduction of daughters in the poor environment, E_1 . This asymmetric effect on R has ramifications for sexual selection, as we show below.

Mothers of genotype B_0B_0 produce $0.5r$ successfully mating sons. Maternal genotypes B_1B_1 and B_1B_0 produce proportions of mating sons equal to $[0.5r + 2(e_1b_1r_1 + e_2b_2r_2)]/f_{\text{males}}$ and $[0.5r + (e_1b_1r_1 + e_2b_2r_2)]/f_{\text{males}}$, respectively. For simplicity, let b_r represent $e_1b_1r_1 + e_2b_2r_2$, the sex ratio bias, weighted by the environment-specific rate of male mating success. In the population, the fraction of breeding males, p_s , relative to all f_{males} is thus

$$p_s = \frac{0.5r + 2pb_r}{0.5 + 2pb}, \quad (4a)$$

$$p_s = \frac{r + 4pb_r}{1 + 4pb}. \quad (4b)$$

Because $r < 1$, p_s is < 1 for all frequencies of the B_1 allele because b_r is always $\leq b$. Thus, the reproductive competition among males results in sexual selection, wherein some fraction of males, $1 - p_s$, are excluded from mating.

The mean reproductive fitness of a successful male equals the product (HW_{female}), where H is the average number of mates of successfully mating males (Wade 1979, 1995; Shuster and Wade 2003). Here,

$$H = \frac{R}{p_s}, \quad (5a)$$

$$\begin{aligned} H &= \frac{1 - 4pb}{r + 4pb_r} \\ &= \frac{2f_{\text{females}}}{r + 4pb_r}. \end{aligned} \quad (5b)$$

Clearly, H is a decreasing function of $0.5(r + 4pb_r)$, male mating success. Differently put, the greater the female bias of the sex ratio (i.e., $b < 0$) and the greater the failure rate of males, the stronger is sexual selection measured by H . When the poor environment is common or mothers in poor condition are abundant, then the excess of daughters produced is large. As this excess of females increases, so does H and, hence, the mean fitness of a successful male, which is the product (HW_{female}).

There are two equivalent ways to calculate the total effects of selection. We can calculate the change in allele frequency, $\Delta p_{\text{maternal}}$, resulting from the variance in mean

fitness of mothers, using brood sex ratios and male mating success to calculate mean brood fitness. Alternatively, we can calculate each member of a series of components of selection that sum to Δp_{total} , the total change in frequency of the B_1 allele. We illustrate both ways in the following sections. The first approach directly converts the verbal TW hypothesis into an evolutionary genetic format and addresses the question, What should a mother do? The second method more clearly illustrates the conflict among the several opposing evolutionary forces in the model and the strength of each force. By isolating the component of sexual selection away from the other two forces, we are able to provide explicit and quantitative confirmation of the TW hypothesis. However, because sexual selection is not the only component affecting the evolutionary dynamic, quantifying the TW effect alone is insufficient to determine whether or not maternal sex-ratio biasing will evolve. Our partitioning shows how the parameter values affect the strength of the opposing evolutionary forces and, thereby, how these three forces combine to determine whether or not total selection favors a biased sex ratio at birth.

Maternal Selection on the B_1 Allele

We first calculate the mean fitness of mothers of each genotype in terms of mean brood fitness and then use these to calculate the change in allele frequency, $\Delta p_{\text{maternal}}$, resulting from selection on mothers. The fitness of a maternal genotype equals the sum of the mean fitness of sons and daughters, each weighted by the fraction of offspring of each sex. We follow the same procedure for each maternal genotype. For example, a B_1B_1 mother produces a fraction of sons equal to $0.5 + 2(e_1b_1 + e_2b_2)$ or $0.5 + 2b$. Of these sons, a fraction, $0.5r + 2(e_1b_1r_1 + e_2b_2r_2)$ or $0.5r + 2b_r$, mate successfully. Similarly, a B_1B_0 mother has a fraction of mating sons equal to $0.5r + b_r$, while a B_0B_0 mother has a fraction of $0.5r$ mating sons.

Next, we calculate the number of mates, H , of a mating male. The value of H is the fraction of females divided by the fraction of mating males, or $(0.5 - 2pb)/(0.5r + 2pb_r)$. Mean male fitness, W_{male} , is HW_{female} . Thus, W_{11} , the fitness of a B_1B_1 mother through her sons and daughters, can be expressed as

$$W_{11} = (\text{frequency of sons})(W_{\text{male}}) \\ + (\text{frequency of daughters})(W_{\text{female}}) \quad (6a)$$

$$= (0.5W_{\text{female}})[(r + 4b_r)H + (1 - 4b)],$$

$$W_{11} = (0.5W_{\text{female}})[1 + rH + 4(b_rH - b)]. \quad (6b)$$

Similarly, we find W_{10} and W_{00} , the fitness of B_1B_0 and B_0B_0 mothers, respectively, are expressed as

$$W_{10} = (0.5W_{\text{female}})[1 + rH + 2(b_rH - b)], \quad (6c)$$

$$W_{00} = (0.5W_{\text{female}})(1 + rH). \quad (6d)$$

Note that the term $(0.5W_{\text{female}})(1 + rH)$ is common to all three genotypes. In order for sex-ratio biasing to enhance maternal fitness, it is necessary that

$$b_rH - b > 0, \quad (7a)$$

$$b_rH > b. \quad (7b)$$

Intuitively, a maternal sex-ratio biasing allele, B_1 , is favored by sexual selection acting on males when the net fitness gained from bias affecting sons, b_rHW_{female} , exceeds that lost from bias affecting daughters, bW_{female} . If we substitute for H in equation (7a) and simplify, we find that B_1 increases maternal fitness when

$$(b_r - br) - 8pb_b > 0. \quad (8)$$

The expression $b_r - br$ is equal to $\text{Cov}(b, r)$, the covariance across environments of the sex-ratio bias toward males and the mating success of sons. It is a covariance because b_r is the mean across environments of the product of the sex-ratio bias and the male mating success, that is, $e_1(b_1r_1) + e_2(b_2r_2)$, minus the product of the mean bias toward sons, b , and the mean mating success of sons, r . (Note that the $\text{Cov}[b, r]$ may be positive even when the average bias, b , is negative, i.e., toward females.)

Maternal sex-ratio biasing evolves whenever

$$\text{Cov}(b, r) > 8pb_b. \quad (9)$$

It is not sufficient that $\text{Cov}(b, r)$ exceeds 0 for selection to favor maternal sex-ratio biasing, as one might conclude from the logic of the TW hypothesis. An association between sex-ratio bias toward sons and male mating success is sufficient for sexual selection to favor sex-ratio biasing but not for total selection to favor it. (We show below how sex ratio biasing is opposed by sex-ratio selection by partitioning total selection into its separate components.)

Noting that $(r + 4pb_r)H$ equals $2f_{\text{females}}$, mean fitness of mothers, W_{mothers} , can be expressed as

$$W_{\text{mothers}} = G_{11}W_{11} + G_{10}W_{10} + G_{00}W_{00}, \quad (10a)$$

$$W_{\text{mothers}} = (0.5W_{\text{female}})[1 + rH + 4p(b_rH - b)], \quad (10b)$$

$$W_{\text{mothers}} = (0.5W_{\text{female}})(4f_{\text{females}}) \\ = (2f_{\text{females}})(W_{\text{females}}). \quad (10c)$$

In the absence of bias, W_{mothers} equals W_{females} , since $2f_{\text{females}}$ equals 1 when b is 0. Sex-ratio bias is the only feature of the model causing variance in fitness among maternal genotypes.

The change in allele frequency, $\Delta p_{\text{maternal}}$, resulting from maternal selection, can be expressed as

$$\Delta p_{\text{maternal}} = \frac{G_{11}W_{11} + (0.5)(G_{10}W_{10})}{W_{\text{mothers}}} - \frac{p(W_{\text{mothers}})}{W_{\text{mothers}}} \quad (11a)$$

or

$$\Delta p_{\text{maternal}} = \frac{(b_r H - b)(0.5W_{\text{female}})[2pq - (G_{10}/2)]}{W_{\text{mothers}}} \quad (11b)$$

The total genic variance in mothers equals $2pq$, while that within mothers equals $(G_{10}/2)$. Thus, the term $2pq - (G_{10}/2)$ is the genetic variance among maternal families, or V_{family} (table 2):

$$\Delta p_{\text{maternal}} = \frac{(b_r H - b)(V_{\text{family}})}{2f_{\text{females}}}, \quad (12a)$$

$$\Delta p_{\text{maternal}} = \frac{[\text{Cov}(b, r) - 8p_B bb_r](V_{\text{family}})}{2f_{\text{females}}}. \quad (12b)$$

This expression is positive as long as $\text{Cov}(b, r) > 8p_B bb_r$. Clearly, mothers biasing brood sex ratio toward sons ($b > 0$) when in good condition but toward daughters in poor condition (i.e., $\text{Cov}[b, r] > 0$) are favored by sexual selection, but it is not a sufficient condition for evolution of the B_1 allele.

Setting equation (12b) equal to 0, we can solve for the equilibrium frequency, p^* , of the sex-ratio biasing allele:

$$p^* = \frac{\text{Cov}(b, r)}{8bb_r}, \quad (13a)$$

$$p^* = \frac{(b_r - br)}{8bb_r}, \quad (13b)$$

$$p^* = \frac{1/b - r/b_r}{8}, \quad (13c)$$

$$p^* = \frac{V_E(b_1 - b_2)(r_1 - r_2)}{8bb_r}. \quad (13d)$$

In these expressions, V_E is the environmental variance, $e_1 e_2$. The expression $(b_1 - b_2)/b$ is Δb , the difference between environments in the relative male bias (i.e., b_1/b and b_2/b), and, similarly, $(r_1 - r_2)/b_r$ is Δr , the difference between environments in the relative fertility of males (i.e., r_1/b_r and r_2/b_r). Thus, we can rewrite equation (13) as

$$p^* = \frac{(V_E)(\Delta b)(\Delta r)}{8}. \quad (14)$$

The quantity Δr is always negative because we have assumed that $r_1 < 0 < r_2$. Since $\Delta r < 0$, this means that Δb must also be negative at genetic equilibrium; that is, the relative bias must be toward females. As Charnov and Bull (1988) argued for ESD, the population sex-ratio bias at birth should be toward the sex produced in the poorer environment. In our case, it is females that are overproduced in the poor environment. Thus, the TW hypothesis not only requires that $\text{Cov}(b, r)$ exceed 0 but also predicts that sexual selection on males will result in a population with a female bias at birth.

At this point, many would argue that, despite the favorable selection on the B_1 allele, sex-ratio selection will oppose any change in the sex ratio at birth and that the sex-ratio bias favored by sexual selection under the TW hypothesis will not be realized. That is not the case. In

Table 2: Sex-specific changes in the frequency of a maternal sex-ratio biasing allele, B_1 , with variance, V

	E_1	E_2	Row average Δp
Males:			
Δp	$+b_1 V/f_{\text{males } E_1}$	$+b_2 V/f_{\text{males } E_2}$	$\Delta p_{\text{males}} = +bV/f_{\text{males}}$
f_{males}	$.5 + 2b_1 p$	$.5 + 2b_2 p$	
Females:			
Δp	$-b_1 V/f_{\text{females } E_1}$	$-b_2 V/f_{\text{females } E_2}$	$\Delta p_{\text{females}} = -bV/f_{\text{females}}$
f_{females}	$.5 - 2b_1 p$	$.5 - 2b_2 p$	
Column average Δp	$\Delta p_{E_1} = 0$	$\Delta p_{E_2} = 0$	$\Delta p = 0$

Note: The parameters, b_1 and b_2 , are the sex ratio biases toward sons in the families of mothers in the poor environment (E_1) and the good environment (E_2), respectively; b is the average bias across all genotypes and environments in the population. Note that because the frequencies of males, f_{males} , and females, f_{females} , sum to 1 in each environment, no net gene frequency change, Δp , is caused by the maternal sex-ratio biasing.

the following sections, we partition total selection into three distinct components: (1) maternal sex-ratio bias, (2) sexual selection, and (3) sex-ratio selection. With this partitioning, it is clear that equation (12) is the sum of all three sources of allele frequency change and includes sex-ratio selection against the B_1 allele. In fact, it is because of the opposing selection that $\text{Cov}(b, r) > 0$ is not a sufficient condition for maternal sex-ratio biasing to evolve. The partitioning also makes it clear why female-biased sex ratios permit more rapid evolution and higher equilibrium values of p^* .

Components of Selection on the B_1 Allele

Our second and equivalent approach to deriving the change in frequency of the B_1 allele is to use the components of selection (table 3). There are three components in this approach: (1) maternal production of broods with different primary sex ratios and the attendant differences in the frequency of B_1 between sons and daughters, (2) sexual selection favoring males from the good environment, and (3) Fisherian sex-ratio selection wherein males and females are equally weighted in producing progeny. We calculate each component in turn and show that they sum to equations (12) above.

Maternal Sex-Ratio Bias

As a result of B_1B_1 and B_1B_0 mothers producing biased sex ratios, the B_1 allele is overrepresented in males and underrepresented in females when $b > 0$. Using table 1, the frequencies of the B_1 allele in sons born in E_1 or in E_2 , $p_{\text{males } E_1}$ and $p_{\text{males } E_2}$, respectively, are $(p_{\text{average}}/2) + b_1[p_{\text{male}}p_{\text{female}} + p_{\text{female}} - (G_{10}/4)]$ and $(p_{\text{average}}/2) + b_2[p_{\text{male}}p_{\text{female}} + p_{\text{female}} - (G_{10}/4)]$. The total change in frequency in males (fig. 2) can be expressed as

$$\Delta p_{B\text{-males}} = + \frac{V_{\text{family}}b}{f_{\text{males}}}, \quad (15a)$$

and, similarly, that in females as

$$\Delta p_{B\text{-females}} = - \frac{V_{\text{family}}b}{f_{\text{females}}}. \quad (15b)$$

These sex-specific allele frequency changes are illustrated in figure 2 for two positive values of b , equal to 0.1 and 0.2. Note that the change is asymmetrical, with Δp_B being smaller in the sex favored by the bias and greater in the sex not favored by it (fig. 2 and table 3). The asymmetry is caused by the effect of the average bias, b , on the denominators of equations (15). Despite this asymmetry, when equations (15a) and (15b) are weighted by f_{males} and f_{females} , respectively, and summed, the total change in the allele frequency is 0 because exchanging males for females and vice versa does not change allele frequency in the progeny as a whole.

Sexual Selection

The second component of selection is sexual selection. Here, all females produce an equal number of offspring, W_{female} , but only a fraction of the males mate successfully. The fraction of all males successful in reproductive competition, p_s , is given in equation (4b). The frequency of the B_1 allele in successfully mating males is

Table 3: The three components of allele frequency change in males and females

	Maternal sex-ratio biasing	Sexual selection	Fisherian selection
Males:			
E_1	$p_{\text{males}} < p$	$p + (Hb_r V)/(f_{\text{females}})$	
E_2	$p_{\text{males}} > p$	$p + (Hb_r V)/(f_{\text{females}})$	
Δp_{males}	$2bV/(1 + 4bp)$	$Hb_r V/f_{\text{females}}$	$\Delta p_{\text{males}}/2$
Females:			
E_1	$p_{\text{females}} > p$	None	
E_2	$p_{\text{females}} < p$	None	
$\Delta p_{\text{females}}$	$-2bV/(1 + 4bp)$	0	$\Delta p_{\text{females}}/2$
Total Δp	0	$V(Hb_r - b)[1 - (1/R)]$	$V[\text{Cov}(b, r) - 8pb_b r]/(2f_{\text{females}})$

Note: Sexual selection changes allele frequencies only in males with harem size of successfully mating males, H ; Fisherian sex-ratio selection = average allele frequency change across both sexes with equal weightings (i.e., $\Delta p_{\text{males}} + \Delta p_{\text{females}})/2$. $\text{Cov}(b, r)$ = covariance between bias, b , and male reproductive success, r , across maternal environments.

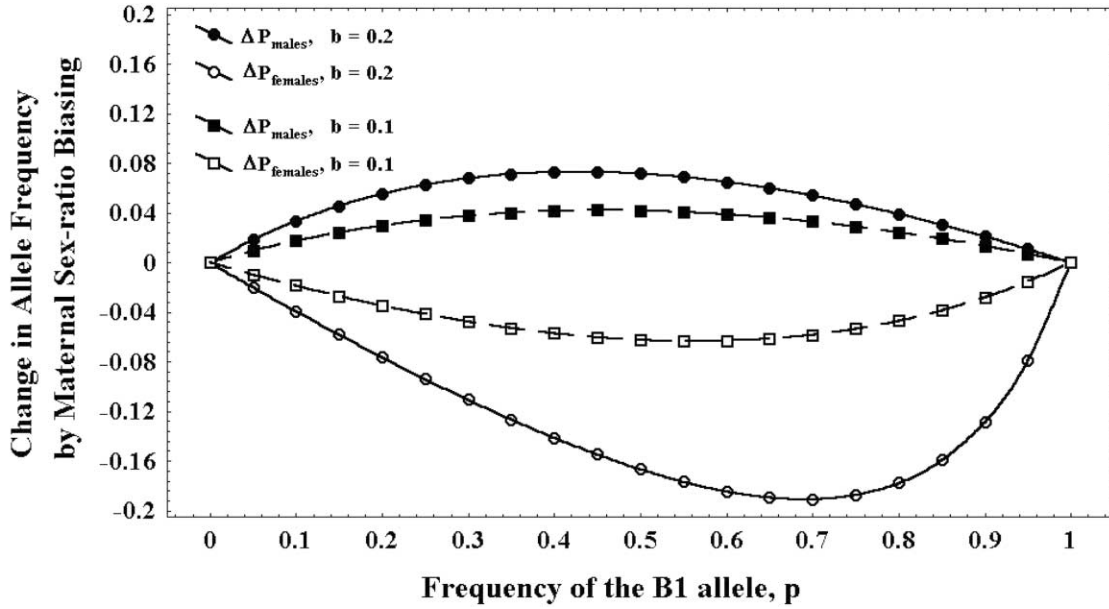


Figure 2: The effect of maternal sex-ratio biasing on the allele frequencies in males and in females. Notice that the changes in frequency of the B_1 allele are asymmetrical, with B_1 overrepresented in the sex favored by the bias (here males) and underrepresented in the other sex (here females).

$$p_{B/S} = \left\{ \left[e_1 r_1 \frac{0.5 + 2b_1 p}{f_{\text{males}}} \right] \left(p + \frac{V_{\text{family}} b_1}{0.5 + 2b_1 p} \right) + \left[e_2 r_2 \frac{0.5 + 2b_2 p}{f_{\text{males}}} \right] \left(p + \frac{V_{\text{family}} b_2}{0.5 + 2b_2 p} \right) \right\} / p_s \quad (16a)$$

$$= p + \frac{2V_{\text{family}} b_r}{r + 4b_r p} \quad (16b)$$

$$= p + \frac{HV_{\text{family}} b_r}{f_{\text{females}}} \quad (16c)$$

The change in allele frequency by sexual selection acting only on males, $\Delta p_{SS\text{males}}$, is

$$\Delta p_{SS\text{males}} = p_{B/S} - \left(p + \frac{V_{\text{family}} b}{f_{\text{males}}} \right), \quad (17a)$$

$$= \frac{V_{\text{family}} H \text{Cov}(b, r)}{2f_{\text{females}} f_{\text{males}}}. \quad (17b)$$

Clearly, sexual selection favors the B_1 allele in males whenever $\text{Cov}(b, r)$ is positive. There is no allele frequency change in females because all females mate and reproduce equal numbers of offspring. The quantity $H \text{Cov}(b, r)$ is an explicit, quantitative expression of the verbal argument behind the TW hypothesis: If there were no other forces changing allele frequency, sexual selection would favor ma-

ternal sex-ratio biasing. The stronger sexual selection as measured by H , the greater is Δp_{SS} , the allele frequency change it causes. However, the third and final component of selection, sex-ratio selection, opposes the biasing allele. Weighting males and females by their respective frequencies, the frequency of B_1 in the entire population (mating males and females), after sexual selection but before offspring production, p_{SS} , equals $p + (V_{\text{family}})[(Hb_r/R) - b]$.

Sex-Ratio Selection

The third and final component of gene frequency change results from sex-ratio selection, which favors the minority sex. The minority sex is the male when the average bias is negative, $b < 0$. However, the allele frequency in males at birth is greater than that of their mothers only if the average bias is positive, $b > 0$. For males to be the minority sex and for p_{B_1} in males to exceed the initial frequency in mothers, sexual selection on males must be strong enough to reverse the negative allele frequency change at birth caused by the maternal sex-ratio bias (table 3).

Although the breeding sex ratio is unequal, there is equal weighting of both sexes in the transmission of the B_1 allele to the offspring. In the production of offspring, the frequencies of the B_1 allele in breeding males, $p_{B/S}$ (from eq. [16c]), and in females, $p_{B\text{-females}}$ are summed and divided by one-half to obtain the final frequency of the B_1 allele, p_{final} , as

$$p_{\text{final}} = p + \frac{(V_{\text{family}})(Hb_r - b)}{2f_{\text{females}}}. \quad (18)$$

The gene frequency change resulting from sex-ratio selection equals

$$\begin{aligned} \Delta p_{\text{Fisher}} &= p_{\text{final}} - p_{\text{SS}} \\ &= V_{\text{family}} \left(\frac{b_r H - b}{2f_{\text{females}}} \right) - V_{\text{family}} \left(\frac{b_r H}{R} - b \right) \end{aligned} \quad (19a)$$

$$= \frac{V_{\text{family}}(b_r H + b)(f_{\text{females}} - f_{\text{males}})}{2f_{\text{females}}}. \quad (19b)$$

By definition, when the average brood is male biased, then b and b_r are positive and $f_{\text{females}} - f_{\text{males}}$ is negative. As a result, equation (19b) is negative. Thus, sex-ratio selection always opposes a male-biasing allele ($\Delta p_{\text{Fisher}} < 0$). In contrast, if the population has a net female bias at birth ($b < 0$) so that $(f_{\text{females}} - f_{\text{males}})$ is positive, it is possible for $\Delta p_{\text{Fisher}} > 0$ if Hb_r is greater than b . When is this so?

According to the TW hypothesis, we have $b_1 < 0 < b_2$ and $r_1 < r_2$. Because $b < 0$, we know that $|e_1 b_1| > |e_2 b_2|$. Thus, for b_r to be positive, r_2/r_1 must exceed 1. When $b < 0$, H is always >1 and, if sufficiently large, $(Hb_r + b)$ can be positive. Thus, sex-ratio selection opposes male-biasing alleles but not necessarily female-biasing alleles. For the TW hypothesis, this means that biases toward sons by mothers in good condition are favored (see ‘‘Discussion’’) only when there is an even more extreme bias toward daughters by mothers in the poor environment.

Total Selection

The total allele frequency change is the sum of the three separate components, or $\Delta p_{\text{total}} = (p_{\text{final}} - p)$. This is the same expression as we found for maternal selection (cf. eqq. [12]):

$$\Delta p_{\text{total}} = \frac{[\text{Cov}(b, r) - 8p_B b b_r](V_{\text{family}})}{2f_{\text{females}}}, \quad (20)$$

where the numerator, $2f_{\text{females}}$, is always >1 for female-biased sex ratios.

Discussion

Several studies provide evidence for an effect of maternal condition on sex ratio in accord with the TW hypothesis (macaques, Paul and Kuester 1987; bison, Wolff 1988; swine, Mendl et al. 1992, 1995, but see Meikle et al. 1997; flycatchers, Ellegren et al. 1996; horses, Monard et al. 1997;

elk, Kohlmann 1999; red deer, Kruuk et al. 1999; birds, Nager et al. 1999). Such studies have been the source of considerable recent debate (Cameron and Linklater 2000, 2002; Carranza 2002). Consistent with our model predictions, in the above species, low-ranking, old, or poorly conditioned mothers were observed to bias broods toward females. Brood sex-ratio variations have been noted in a wide variety of other taxa, but the processes driving this tendency have seldom been unambiguously identified (see the review by West and Sheldon 2002).

Our model has several implications for the experimental investigation of maternal sex-ratio biasing. First, the observation of significant variation among brood sex ratios alone is insufficient evidence for adaptive maternal sex-ratio biasing. Like the TW hypothesis, we predict a positive covariance between brood sex-ratio bias and reproductive success of sons. In experimental systems, our prediction could be tested by nutritional manipulation of maternal condition and subsequent observation of both brood sex ratio and average son reproductive success. These should covary positively across maternal families if sexual selection has been involved in the maternal sex-ratio biasing. Second, our model predicts low levels of genetic variation to exist in populations for the ability to vary sex ratio unless the difference between good and poor environments is large for both relative bias and sons’ relative fitness (eq. [14]). Thus, it would be strategically advantageous to undertake a nutritional manipulation of maternal condition before investigation of the heritability of the maternal sex-ratio effect. Third, where there is significant heritable variation for the maternal effect, we would expect the variation to be lost if sexual selection were eliminated. Sexual selection could be halted by artificially eliminating the among-family variance in male reproductive success. Conversely, sexual selection could be enhanced by artificially augmenting the among-family variance in male reproductive success.

The evolution of maternal sex-ratio biasing involves the simultaneous action of three sometimes opposing evolutionary processes: (1) maternal sex-ratio biasing, which creates a sex difference in gene frequency at birth; (2) sexual selection, which favors males from good environments over those from poor ones; and (3) sex-ratio selection, which favors genes in the minority sex. In the absence of sexual selection, processes (1) and (2) are opposed to one another because the sex favored by the maternal bias is enriched for a biasing gene, while the minority sex, favored by sex-ratio selection, has a reduced frequency of the biasing gene. The TW hypothesis discusses only how maternal sex-ratio biasing can be favored by sexual selection without explicitly or quantitatively discussing the opposing force of sex-ratio selection. The evolutionary process is further complicated by the fact that

in evolutionary genetic theory, indirect maternal effects and direct but sex-limited sexual selection are weighted differently (Wolf and Wade 2001). Additionally, sex-ratio selection is frequency dependent and varies in strength depending on the degree of sex-ratio bias. It is unlikely that verbal arguments alone could appropriately weight each of these simultaneously acting but opposing processes. Pen and Weissing (2000, p. 59) advocate evolutionarily stable strategy (ESS) models of sex ratio and sexual selection on the grounds that "In comparison with population genetic and quantitative genetic models of sexual selection, the ESS approach is simpler and yields more insight in the underlying selective forces." However, it has been shown that game theoretical approaches do not function well in discriminating direct from indirect selection when both are operating simultaneously (e.g., Wolf and Wade 2001; Wade and Shuster 2002).

Our model provides a more quantitative format for investigating these forces in a common framework. In particular, we derive a quantitative statement of the verbal TW hypothesis (eq. [17b]), which illustrates that a positive covariance between sex-ratio biasing and male reproductive success ($\text{Cov}[b, r] > 0$) is a necessary but not sufficient condition for the evolution of maternal sex-ratio biasing. The strength of sexual selection (H) is a direct multiplier of this covariance. Because sexual selection can be stronger with female-biased sex ratios (i.e., H is larger), it is easier and faster to evolve female-biased sex ratios under the TW hypothesis. This asymmetry is not apparent in the original verbal model of the TW hypothesis as evidenced by the following interpretation: "If parental manipulation of the sex ratio is a device for maximizing reproductive success, parents in poor condition should favor daughters to the *same extent* that parents in good condition favor sons" (Hawkes 1981, p. 86, our emphasis). The expectation from the TW hypothesis of biasing to equal extent is not met because the strength of sexual selection is differentially affected by female biases ($b < 0$) as opposed to male biases ($b > 0$) of the same magnitude. The asymmetry is particularly important given opposing sex-ratio selection (eq. [19b]). Sex-ratio selection never favors a gene that biases brood sex ratio toward males, but, given a sufficiently large difference between environments in male reproductive success, it can favor female-biased brood sex ratios. Thus, the two forces, sexual selection and sex-ratio selection, can act together to favor female-biased broods but not male-biased broods.

Our model could be altered in many ways. Instead of equal family size, we could permit mothers in poor condition to have fewer offspring (N_1) than mothers in good condition (N_2), as discussed by Trivers and Willard (1973). Since females of all genotypes experience the two environments in the same proportions, mean family size, N ,

would be equal to $e_1N_1 + e_2N_2$, but there would be no covariance between female genotype and family size. The frequency of the contributions of each environment to overall offspring production would no longer be e_1 and e_2 but $e'_1 (= e_1[N_1/N])$ and $e'_2 (= e_2[N_2/N])$. That is, the frequencies of the environments would be weighted by the relative family fitness in each. Effectively, this makes the poor environment, E_1 , relatively rarer, because $(N_1/N < 1)$, and the good environment, E_2 , relatively more common, since $N_2/N > 1$. When e'_1 and e'_2 are substituted for e_1 and e_2 in $e_1b_1 + e_2b_2$, the average bias, b , is decreased when $b_1 < 0 < b_2$, causing a parallel decrease in Δb in equation (14). The difference, $f_{\text{females}} - f_{\text{males}}$ or $-4pb$, which governs Δp_{Fisher} , is affected in the same way. Thus, environment-induced differences in family size are equivalent to diminishing the experience of E_1 and enhancing the experience of E_2 and so reduce the likelihood that maternal sex-ratio biasing will evolve.

Maternal habitat selection dependent on maternal condition could be another way to modify our model. In this case, the realized brood sex-ratio bias would be increased if mothers in poor condition sought out poor environments in which to reproduce but diminished if they sought out good environments. Nonrandom mating within habitats would also further complicate the evolutionary dynamics.

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