

Haplodiploidy, Sex-Ratio Adjustment, and Eusociality

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ABSTRACT: Hamilton's "haplodiploidy hypothesis" holds that inflated sororal relatedness has promoted altruistic sib rearing in haplodiploids, potentially explaining their apparent predisposition to eusociality. Here, we suggest that haplodiploidy may instead promote eusociality simply by facilitating sex-ratio adjustment. Specifically, haplodiploidy may enable sex-ratio bias toward the more helpful sex, owing to "local resource enhancement," and such sex-ratio bias may promote the evolution of helping by individuals of that sex, owing to the "rarer-sex effect." This could explain why haplodiploidy appears to have been important for eusociality in taxa with only female helpers, such as ants, wasps, and bees, but not in taxa with both male and female helpers, such as termites.

Keywords: inclusive fitness, kin selection, local resource enhancement, rarer-sex effect, sex allocation, social insects.

Unfertilized eggs always turn into males, fertilized into females. Whether an egg shall be fertilized or no is controlled by the queen as she lays it. ... There is a reason for this. The ordinary methods of sex-determination inevitably give equal proportions of males and females. But the states of ant, bee and wasp are based on the labour of sterilized females. What should they do with a huge population of useless males, when a few score are ample to perpetuate the race? The problem has been neatly solved by the adoption of this other method, in which the proportion of the sexes can be varied as desired. (Wells et al. 1929, p. 778)

Introduction

Obligate eusociality is a permanent division of reproductive labor whereby both reproductive and helper castes are required for complementary totipotency (Crespi and Yanega 1995; Boomsma et al. 2011). This system of biological organization is known only in the haplodiploid

social hymenoptera (ants, wasps, and bees) and the diploid termites (Boomsma et al. 2011). The apparent predisposition of taxa with haplodiploid sex determination—in which diploid females develop from fertilized eggs and haploid males develop from unfertilized eggs—to eusociality has generated much interest. Hamilton (1964, 1972) famously suggested that this owes to the inflated relatedness of full sisters under haplodiploidy ($r = 3/4$, rather than the usual $r = 1/2$ under diploidy), promoting the evolution of altruistic sib rearing in haplodiploid taxa. However, this "haplodiploidy hypothesis" has gradually fallen out of favor, for both theoretical and empirical reasons (reviewed by Gardner et al. 2012).

An alternative possibility is that haplodiploid sex determination promotes eusociality simply by facilitating sex-ratio adjustment. Sex-ratio bias may be favored when offspring of only one sex provide help to their mother, termed "local resource enhancement" (Wells et al. 1929; Trivers and Willard 1973; Frank 1998; Pen and Weissing 2000; West 2009). Moreover, since reproductive value is lower for individuals of the more common sex—the "rarer-sex effect" (Fisher 1930; West 2009)—the effective cost of helping is reduced when there is sex-ratio bias toward the more helpful sex, which may favor those individuals to invest even more into helping. This positive feedback between sex-ratio bias and sex-biased helping could lead to exaggerated altruism, with a significant fraction of individuals devoting their lives to sib rearing, but only insofar as sex ratios are evolutionarily labile. Haplodiploidy is known to allow for remarkable precision of sex-ratio adjustment (Wells et al. 1929; Maynard Smith 1978; Bull 1983; West 2009) and may consequently have promoted the evolution of eusociality.

Here, we formalize this hypothesis using the mathematical tools of kin selection theory (Hamilton 1963, 1964, 1970, 1972; Taylor 1990; Taylor and Frank 1996; Frank 1997, 1998; Rousset 2004; Taylor et al. 2007). We develop a mathematical model in which mothers may engage in sex-ratio adjustment and juvenile females may choose to devote their lives to sib rearing, to explore the coevolution

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of sex ratio and female-biased helping under both diploid and haplodiploid modes of inheritance. We also survey empirical data on helper sex ratios and the genetic systems of both obligate and facultative eusocial taxa and their closest nonsocial relatives. Our aim is to assess, both theoretically and empirically, the impact that effective sex-ratio adjustment has on the evolution of eusociality based on female altruism.

Analysis

Model

We develop a model of costly sex-ratio adjustment, in which there is a trade-off between the number and sex of a mother's offspring, and costly sib rearing, in which there is a trade-off between helping and personal reproduction. For simplicity, we focus on unbiased and female-biased sex ratios, as male-biased sex ratios are never favored in the context of our model. We assume diploid or haplodiploid inheritance, with strict monogamy and no inbreeding.

We consider that a mother interferes with the sex determination of a proportion a of her eggs, rendering the egg inviable with probability c and successfully producing a daughter with probability $1 - c$, and she leaves the sex determination of a proportion $1 - a$ of her eggs to chance, half of which will develop as daughters and half as sons. As a result, a proportion $(1 - c)/[1 - 2c(1 - x)]$ of her eggs are viable, and a proportion $x = [1 - a + 2a(1 - c)]/(2 - 2ac)$ of these viable eggs develop as daughters (where $x \geq 1/2$). Our key assumption is that c is low (perhaps 0) for haplodiploids and is higher for diploids. We also consider that females engage in altruistic sib rearing. A focal juvenile survives to adulthood with probability $S(h)$, where $h = xY$ is the proportion of siblings developing as nonreproductive helpers: a proportion x of siblings are sisters, and a proportion Y of sisters develop as helpers. On reaching adulthood, a focal female develops as a helper with probability y and as a reproductive with probability $1 - y$. In contrast, all males develop as reproductives.

Evolution of Sex Ratio

We find that natural selection acts to increase the degree of female bias in the sex ratio when

$$\frac{1}{\bar{x}} - \frac{1}{1 - \bar{x}} - \frac{4c}{1 - 2c(1 - \bar{x})} + 2s\bar{y} > 0, \quad (1)$$

where $s = (dS/dh)/S(h)|_{h=\bar{x}\bar{y}}$ is the marginal relative survival benefit of receiving help from siblings (see the appendix for derivation). This condition holds for both diploid

and haplodiploid inheritance but is less stringent under haplodiploidy if this entails a lower cost of sex-ratio adjustment (lower c).

The $1/\bar{x} - 1/(1 - \bar{x})$ term on the left-hand side of inequality (1) represents the rarer-sex effect (Fisher 1930; West 2009). This is negative for all $\bar{x} > 1/2$, which acts to reduce the extent of any female bias. The $-4c/[1 - 2c(1 - \bar{x})]$ term represents the mortality cost of sex-ratio bias, which also acts to reduce the extent of any female bias. And the $2s\bar{y}$ term represents the local-resource-enhancement effect (Wells et al 1929; Trivers and Willard 1973; Pen and Weissing 2000; West 2009), which acts to promote female bias provided that females improve the survival of siblings ($s\bar{y} > 0$).

If sex-ratio adjustment is costless ($c = 0$), then the convergence stable (Eshel and Motro 1981; Christiansen 1991; Taylor 1996) sex ratio is $x^* = 1/[1 - s\bar{y} + [1 + (s\bar{y})^2]^{1/2}]$, which increases monotonically from $x^* = 1/2$ to $x^* \rightarrow 1$ as the helpfulness of females increases from $s\bar{y} = 0$ to $s\bar{y} \rightarrow \infty$. In contrast, if sex-ratio adjustment is always lethal ($c = 1$), then the convergence stable sex ratio is $x^* = 1/2$. An analytical solution is available for intermediate cost of sex-ratio adjustment ($0 < c < 1$), but it is too cumbersome to reproduce here. Figure 1A illustrates how female-biased helping favors female-biased sex ratios, especially when the cost of sex-ratio adjustment is small or absent.

Evolution of Helping

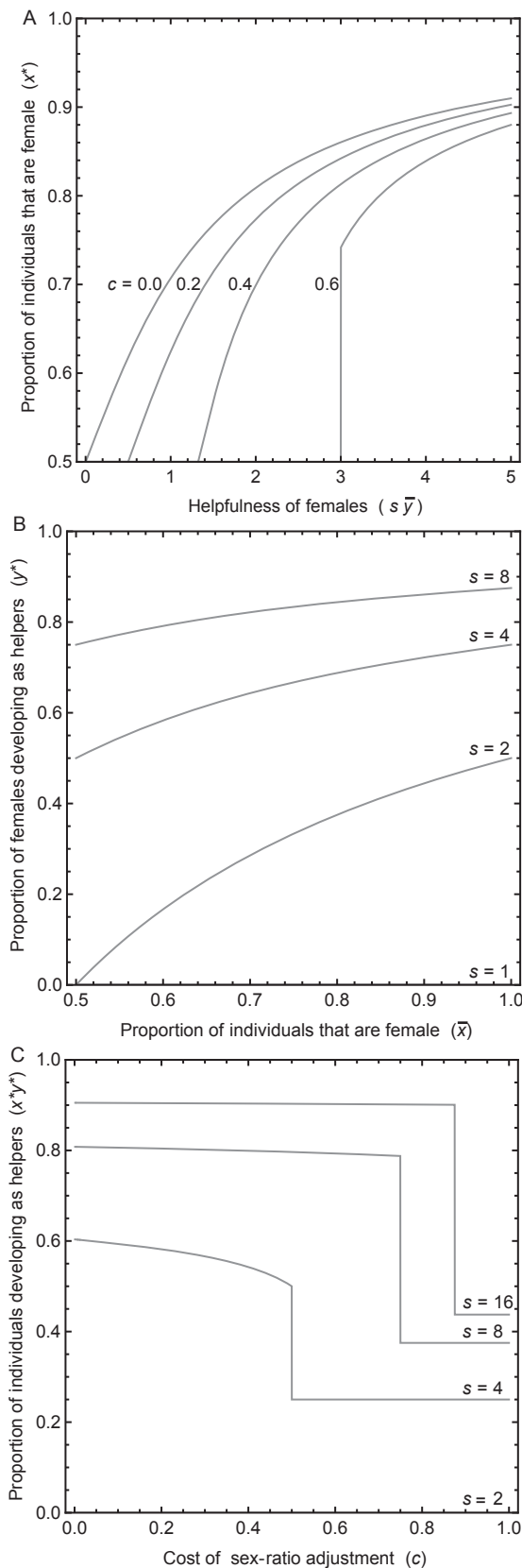
We find that natural selection acts to increase the proportion of females developing as helpers when

$$-\frac{1}{\bar{x}(1 - \bar{y})} + s > 0, \quad (2)$$

(see the appendix for derivation). Again, this condition holds for both diploid and haplodiploid inheritance.

The $-1/\bar{x}(1 - \bar{y})$ term on the left-hand side of inequality (2) represents the direct cost of helping, which acts to inhibit helping. A fraction $\bar{x}(1 - \bar{y})$ of individuals surviving to adulthood are reproductive females, and hence the reproductive value lost by developing as a helper is inversely proportional to this fraction. The s term represents the helping benefit to siblings, which acts to promote helping.

Irrespective of the cost of sex-ratio adjustment, the convergence stable level of female helping is $y^* = \min[(s\bar{x} - 1)/s\bar{x}, 0]$. That is, it is a monotonically increasing function of the product of the survival benefit of helping s and the sex ratio \bar{x} . Specifically, $y^* = 0$ for $0 \leq s\bar{x} \leq 1$, and $y^* \rightarrow 1$ as $s\bar{x} \rightarrow \infty$. Figure 1B illustrates how a female-biased sex ratio favors female-biased helping, especially when the survival benefit of helping is large.



Coevolution of Sex Ratio and Helping

Natural selection favors an increase in both the proportion of offspring that are female and the proportion of females that develop as helpers when both inequalities (1) and (2) are satisfied. If sex-ratio adjustment is costless ($c = 0$), then this leads to an unbiased sex ratio $x^* = 1/2$ and the absence of sib rearing $y^* = 0$ when the survival benefit of helping is $s \leq 2$ and to a female-biased sex ratio $x^* = 1/[s - [s(s - 2)]^{1/2}]$ and a relatively large proportion of females developing as helpers $y^* = [(s - 2)/s]^{1/2}$ when the survival benefit is $s > 2$. In contrast, if sex-ratio adjustment is lethal ($c = 1$), then this leads to an unbiased sex ratio $x^* = 1/2$ and the absence of sib rearing $y^* = 0$ when the survival benefit of helping is $s \leq 2$ and to an unbiased sex ratio $x^* = 1/2$ and a relatively small proportion of females developing as helpers $y^* = (s - 2)/s$ when the survival benefit is $s > 2$. Analytical solutions are available for intermediate cost of sex-ratio adjustment ($0 < c < 1$), but they are too cumbersome to reproduce here. In general, both the sex ratio and the proportion of females developing as helpers are monotonically decreasing functions of the cost of sex-ratio adjustment ($dx^*/dc < 0$ and $dy^*/dc < 0$).

Of particular interest is the total proportion of offspring developing as helpers, that is, $h^* = x^*y^*$. For costless sex-ratio adjustment ($c = 0$), this is $h^* = 0$ for $s \leq 2$ and $h^* = [(s - 2)/s]^{1/2}/[s - [s(s - 2)]^{1/2}]$ for $s > 2$. For lethal sex-ratio adjustment ($c = 1$), this is $h^* = 0$ for $s \leq 2$ and $h^* = (s - 2)/(2s)$ for $s > 2$. That is, the proportion of offspring developing as helpers under costless sex-ratio adjustment is at least double that which occurs in the absence of sex-ratio adjustment. Numerical illustrations, including for intermediate cost of sex-ratio adjustment ($0 < c < 1$) are given in figure 1C. Consequently, if haplodiploids suffer a lower cost of sex-ratio adjustment than do diploids, we predict that haplodiploidy will promote the evolution of sib rearing in societies that exhibit female-biased helping.

Empirical Survey

We consider the scope for the sex-ratio-adjustment hypothesis to explain the incidence of eusociality across the range from primitive to obligate eusociality (table 1). We

Figure 1: Haplodiploidy promotes eusociality by facilitating sex-ratio adjustment. *A*, Increasingly helpful females (large $s\bar{y}$) favor increasingly female-biased sex ratios (large x^*), but only insofar as sex-ratio adjustment is effective (low c). *B*, Increasingly female-biased sex ratios (large \bar{x}) favor increasingly helpful females (large y^*). *C*, This positive feedback between female-biased sex ratio (\bar{x}) and female-biased helping (\bar{y}) increases the proportion of individuals developing as helpers (large $h^* = x^*y^*$), but only insofar as mechanisms such as haplodiploidy are available to facilitate sex-ratio adjustment (low c).

compare helper and total-brood sex ratios within eusocial taxa as well as between eusocial taxa and their closest nonsocial relatives. We find that eusocial taxa with a female-biased worker caste—and hence potential for a female-biased sex ratio to be favored by local resource enhancement—either are ancestrally haplodiploid (social hymenoptera, ambrosia beetles) or evolved from ancestors that already had strongly female-biased sex allocation, probably owing to local mate competition (social spiders; Choe and Crespi 1997) or as a consequence of cyclic parthenogenesis (eusocial aphids; Choe and Crespi 1997).

Eusocial taxa that have a mixed-sex worker caste, possibly owing to their ancestors having biparental care (termites, mole rats) and/or their workers mainly having a defensive rather than a caring role (thrips, sponge-dwelling shrimp, primitive termites), have no such requirement for a female-biased sex ratio. The absence of single-sex helping among eusocial taxa that lack a preexisting sex-ratio-adjustment mechanism (haplodiploidy or otherwise) suggests that the evolution of eusociality is constrained by the ability to adjust sex ratio.

Discussion

We have suggested that haplodiploid sex determination may promote the evolution of eusociality by facilitating sex-ratio adjustment. We have provided theoretical support for this idea by showing that the proportion of individuals developing as altruistic helpers increases with ease of sex-ratio adjustment (lower c) when helping is female biased. This owes to (1) a female-biased sex ratio being favored when helping is female biased (owing to local resource enhancement; Wells et al. 1929; Trivers and Willard 1973; Frank 1998; Pen and Weissing 2000; West 2009) and (2) exaggerated female-biased helping being favored when the sex ratio is female biased (owing to the rarer-sex effect; Fisher 1930; West 2009). We have also provided empirical support for this idea, showing that all eusocial taxa with female-biased helping produce female-biased sex ratios and either are haplodiploid or evolved sex-ratio bias prior to helping.

Our hypothesis is inspired by the suggestion of H. G. Wells, Julian Huxley, and G. P. Wells (Wells et al. 1929) that haplodiploid sex determination arose in the context of hymenopteran societies as a means of facilitating sex-ratio bias toward the more helpful sex. While this is clearly naïve—haplodiploidy is ancestral and eusociality is derived, rather than vice versa—we have been able to rework their suggestion so that haplodiploidy is instead viewed as preadapting the hymenoptera to eusociality by facilitating sex-ratio adjustment. Moreover, their remark may represent the earliest statement of the logic of local resource enhancement (Trivers and Willard 1973; Pen and Weissing

2000; West 2009). Frank (1998, pp. 235–238) provides an excellent overview of sex-ratio bias resulting from sex-biased helping, highlighting (though not exploring) the evolution of helping itself. We have shown that sex-ratio bias resulting from female-biased helping acts to promote female-biased helping, owing to the rarer-sex effect (Fisher 1930; West 2009), and that the resulting positive feedback may drive exaggerated altruistic sib rearing. Frank and Crespi (1989) describe an alternative mechanism that yields a similar synergistic, eusociality-promoting effect.

Our mathematical model makes a number of key assumptions. First, we have assumed that individuals are outbred. Relaxing this assumption would increase the relative value of daughters versus sons under haplodiploidy but not under diploidy, which could act to promote the impact of haplodiploidy on eusociality via sex-ratio evolution. Significant inbreeding appears to have been absent at the origin of eusociality in the social hymenoptera (Boomsma 2009) but may have been important in the evolution of eusocial thrips (Chapman et al. 2000). Second, we have assumed the complete absence of multiple mating. Strict monogamy facilitates altruistic sib rearing, as it ensures that potential helpers are as related to their maternal siblings as they are to their own offspring (Boomsma 2007, 2009). Although multiple mating is known among eusocial organisms—the honeybee being a notable example—this is understood to be a derived condition that evolved subsequently to the establishment of eusociality under strict monogamy (Hughes et al. 2008; Boomsma et al. 2011).

Third, we have made the crucial assumption that one sex does more helping than the other. The societies of the social hymenoptera do rest on the labor of female workers, probably owing to their eusociality having evolved out of maternal care. Specifically, the ancestors of modern social hymenoptera exhibited maternal but not paternal care, making females preadapted to working by simply diverting nursing behavior away from their own offspring and toward their siblings (Wheeler 1928). In contrast, termites differ from the social hymenoptera in having approximately equal numbers of female and male workers. This may be owing to their altruism having originally taken the form of soldiering rather than nursing and hence neither sex being particularly preadapted to the worker condition. Interestingly, their sister clade, *Cryptocercus*, shows evidence of biparental care (Klass et al. 2008), which may also explain the absence of sex-biased helping. Thus, termites may be the exception that proves the rule: their path to eusociality has obviated the need for sex-ratio adjustment, and hence their diploidy has not presented a barrier to exaggerated altruism. More generally, surveying taxa with a range of degrees of eusociality (table 1), we suggest that ability and need for sex-ratio adjustment are better

Table 1: Estimates of salient life-history traits for known eusocial taxa (left) and their nonsocial sister taxa (right)

	Eusocial taxa				Closest non-eusocial relatives				Reference(s)	
	Taxonomic group	Ploidy	Sex of helpers	Sex ratio bias?	Closest relative	Ploidy	Parental care?	Sib mating?		Sex ratio bias?
Obligately eusocial taxa	Termites: single origin	Diploidy	Both sexes (generally no sex bias in division of labor, but variable among lineages)	Unbiased (for both workers and reproductives), but biased in the soldier caste in some taxa	Wood roach: <i>Cryptocercus</i> spp.	Diploidy	Biparental care	Low-level inbreeding, but few data	Unbiased, but few data	Muller and Korb 2008; Thorne 1997; Inward et al. 2007; Klass et al. 2008
	Hymenoptera: obligately eusocial taxa (some wasps, some bees, all ants), 3 origins	Haplodiploidy	Females	Workers are strongly female biased, reproductives are mixed	Hymenoptera: semisocial taxa (some wasps and bees)	Haplodiploidy	Maternal provisioning in many taxa (direct and indirect)	Yes in some taxa, but not those that gave rise to eusociality	Yes, bias and flexible sex ratios in many taxa	Hölldobler and Wilson 1990
Facultatively eusocial taxa	Hymenoptera: facultatively eusocial taxa (some wasps and bees), multiple origins	Haplodiploidy	Females	Nonreproductives are female only, reproductives are mixed	Hymenoptera: semisocial taxa (some wasps and bees)	Haplodiploidy	Maternal provisioning in many taxa (direct and indirect)	Yes in some taxa, but not those that gave rise to eusociality	Yes, bias and flexible sex ratios in many taxa	Choe and Crespi 1997; Michener 1974
	Ambrosia beetles: <i>Austroplatypus incompertus</i> , possibly obligately eusocial	Diploidy	Mainly females, but males might help a little (few data)	Equal sex ratio among dispersers, but females outnumber males in established colonies (few data)	Ambrosia beetles: Platypodinae	Haplodiploidy, diploidy, and paternal genome elimination	Biparental care and cooperative breeding (mainly female helpers)	No	No bias	Kent and Simpson 1992; Kent 2002
	Ambrosia beetles: <i>Xyleborinus saxessii</i>	Haplodiploidy	Mainly females (both larvae and adults), but males might help a little	Yes, strongly female biased owing to local mate competition	Ambrosia beetles: Xyleborini	Haplodiploidy	Maternal care and cooperative breeding (mainly female helpers)	Yes, extreme local mate competition	Yes, strongly female biased	Biedermann and Taborsky 2011; Choe and Crespi 1997

Social spiders: "eusocial" taxa	Diploidy	Females	Yes, strongly female biased	Social spiders: semisocial taxa	Diploidy	Maternal care and cooperative breeding (female helpers)	Yes	Yes, strongly female biased	Choe and Crespi 1997
Eusocial aphids: 50 species in 2 related families, 6+ evolutionary transitions	Diploidy (but many females produced by parthenogenesis)	Females (asexuals), defense only (no brood care)	Yes (all-female clonal colony)	Nonsocial aphids	Diploidy but with cyclic parthenogenesis	No	...	Yes (as most asexuals are females)	Choe and Crespi 1997
Eusocial thrips: gall thrips, 1-2 origins	Haplodiploidy	Both sexes, defense only (no brood care)	Soldier generation lacks strong bias (52% male), dispersing generation has extreme female bias (5.6% male)	Nonsocial gall thrips	Haplodiploidy	No	High inbreeding in those taxa giving rise to eusociality	Strongly female biased among those individuals that mate prior to dispersal, no bias among those that do not	Choe and Crespi 1997; Chapman et al. 2000
African mole rats: <i>Heterocephalus glaber</i> , <i>Cryptomys damarensis</i> , 2 independent origins	Diploidy	Both sexes, including both parents	No primary sex-ratio bias, slight male bias among adults	African mole rats: solitary and cooperative breeders	Diploidy	Both sexes help and fathers stay around and help as well	High levels of inbreeding, but outbreeding preference and inbreeding depression	No primary sex ratio bias, slightly male biased among adults	Jarvis 1981; Bennett and Faulkes 2000
Sponge-dwelling shrimp: <i>Synalpheus</i> spp., 3 independent origins	Diploidy (with possible sequential hermaphroditism in some species)	Both sexes	Roughly equal sex ratios, but in some species 0%-100% of helpers and queens are intersex (both male and female reproductive organs)	Sponge-dwelling shrimp: solitary taxa	Diploidy (with possible sequential hermaphroditism)	Socially monogamous pairs, biparental care suggested for some species	No suggestion of sibmating (but few data)	Even sex ratio? (few data and unclear owing to possible sex change)	Duffy 1996; Toth and Bauer 2007, 2008

predictors of the distribution of eusociality than is haplodiploidy per se.

There are strong reasons for suspecting that haplodiploidy does facilitate sex-ratio adjustment. An unbiased sex ratio is typically the default under diploid chromosomal sex determination (Bull 1983), and while disruption of the usual segregation of sex-ratio alleles does provide a means of sex-ratio adjustment (West 2009), this is liable to be associated with costs. In contrast, there is no default sex ratio under haplodiploidy: here, an unbiased sex ratio already requires remarkable precision in the control of which eggs are to be fertilized. However, empirical support for these ideas is relatively lacking. West et al.'s (2005) meta-analysis suggests that chromosomal sex determination is associated with reduced sex-ratio bias in vertebrates but not in insects, although this analysis confounds the ability to adjust sex ratio with the selection pressures for sex-ratio bias (West et al. 2005). A more profitable avenue for future exploration may be to apply selection for female-biased sex ratios to laboratory populations of haplodiploid versus diploid representatives of the same taxa and directly measure the evolutionary response.

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APPENDIX

Evolution of Sex Ratio and Helping

The expected fitness of a focal daughter is $w_f = x(1 - c)/[1 - 2c(1 - x)]S(xY)(1 - \gamma)k_f$, and the expected fitness of a focal son is $w_m = (1 - x)(1 - c)/[1 - 2c(1 - x)]S(xY)k_m$, where k_f and k_m are the expected fitnesses of a reproductive female and a reproductive male, respectively. The population averages of these are $\bar{w}_f = \bar{x}(1 - c)/[1 - 2c(1 - \bar{x})]S(\bar{x}\bar{Y})(1 - \bar{\gamma})k_f$ and $\bar{w}_m = (1 - \bar{x})(1 - c)/[1 - 2c(1 - \bar{x})]S(\bar{x}\bar{Y})k_m$. The condition for natural selection to favor an increase in the population average of any heritable trait is $c_f dW_f/dg_f + c_m dW_m/dg_m > 0$, where c_f and c_m are the class reproductive values of females and males, respectively (i.e., $c_f = c_m = 1/2$ under diploidy and $c_f = 2/3$ and $c_m = 1/3$ under haplodiploidy; Price 1970; Taylor 1996); $W_f = w_f/\bar{w}_f$ and $W_m = w_m/\bar{w}_m$ are the relative fitnesses of females and males, respectively; the de-

derivatives are evaluated at the population average trait values (i.e., $x = \bar{x}$ and $y = Y = \bar{y}$); and g_f and g_m denote the genic values of a gene drawn at random from the focal locus of a female and male, respectively (Taylor 1996; Taylor and Frank 1996; Frank 1997, 1998; Taylor et al. 2007).

Taking the proportion of offspring that are female as our trait of interest, we have $dW_f/dg_f = (\partial W_f/\partial x) \times (dx/dG') \times (dG'/dg_f)$, where dx/dG' is the mapping between the focal daughter's mother's breeding value G' and her sex-ratio strategy x , which can be arbitrarily set to unity, and dG'/dg_f is the consanguinity of the focal daughter to her mother, p' (i.e., $p' = 1/4$ under both diploidy and haplodiploidy; Bulmer 1994; Taylor and Frank 1996). Similarly, we have $dW_m/dg_m = (\partial W_m/\partial x) \times (dx/dG') \times (dG'/dg_m)$, where dG'/dg_m is the consanguinity of the focal son to his mother, q' (i.e., $q' = 1/4$ under diploidy and $q' = 1/2$ under haplodiploidy). Making these substitutions into the condition $c_f dW_f/dg_f + c_m dW_m/dg_m > 0$ yields inequality (1) of the main text.

Taking the proportion of females developing as helpers as our trait of interest, we have $dW_f/dg_f = (\partial W_f/\partial \gamma) \times (d\gamma/dG) \times (dG/dg_f) + (\partial W_f/\partial Y) \times (dY/dG'') \times (dG''/dg_f)$, where $d\gamma/dG$ is the mapping between the focal daughter's breeding value G and her helping strategy γ , which can be arbitrarily set to unity; dY/dG'' is the mapping between the focal daughter's sisters' average breeding value G'' and their average helping strategy Y , which takes the same value; dG/dg_f is the consanguinity of the focal daughter to herself, p (i.e., $p = 1/2$ under both diploidy and haplodiploidy); and dG''/dg_f is the consanguinity of the focal daughter to her sister, p'' (i.e., $p'' = 1/4$ under diploidy and $p'' = 3/8$ under haplodiploidy). Similarly, we have $dW_m/dg_m = (\partial W_m/\partial Y) \times (dY/dG'') \times (dG''/dg_m)$, where dG''/dg_m is the consanguinity of the focal son to his sister, q'' (i.e., $q'' = 1/4$ under diploidy and $q'' = 1/2$ under haplodiploidy). Making these substitutions into the condition $c_f dW_f/dg_f + c_m dW_m/dg_m > 0$ yields inequality (2) of the main text.

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