

# Spiteful Soldiers and Sex Ratio Conflict in Polyembryonic Parasitoid Wasps

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**ABSTRACT:** The existence of spiteful behaviors remains controversial. Spiteful behaviors are those that are harmful to both the actor and the recipient, and they represent one of the four fundamental types of social behavior (alongside selfishness, altruism, and mutual benefit). It has generally been assumed that the conditions required for spite to evolve are too restrictive, and so spite is unlikely to be important. This idea has been challenged in recent years, with the realization that localized competition can relax the conditions required for spite to evolve. Here we develop a theoretical model for a prime candidate for a spiteful behavior, the production of the sterile soldier caste in polyembryonic wasps. Our results show that (a) the biology of these soldiers is consistent with their main role being to mediate conflict over the sex ratio and not to defend against competitors and (b) greater conflict will occur in more outbred populations. We also show that the production of the sterile soldier caste can be classed as a spiteful behavior but that, to an extent, this is merely a semantic choice, and other interpretations such as altruism or indirect altruism are valid. However, the spite interpretation is useful in that it can lead to a more natural interpretation of relatedness and facilitate the classification of behaviors in a way that emphasizes biologically interesting differences that can be empirically tested.

**Keywords:** spite, altruism, Hamilton's rule, relatedness, reproductive value, *Copidosoma*.

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Behaviors that reduce the fitness of the actor pose a problem for evolutionary theory. Hamilton's (1963, 1964) inclusive fitness theory provides an explanation for such behaviors by showing that they can be favored because of their effects on relatives. This is encapsulated by Hamilton's (1963, 1964) rule, which states that a behavior will be favored when  $rb > c$ , where  $c$  is the fitness cost to the actor,  $b$  is the fitness benefit to the recipient, and  $r$  is their genetic relatedness. Hamilton's rule provides an explanation for altruistic behaviors, which give a benefit to the recipient ( $b > 0$ ) and a cost to the actor ( $c > 0$ ): altruism is favored if relatedness is sufficiently positive ( $r > 0$ ) so that  $rb - c > 0$ . The idea here is that by helping a close relative reproduce, an individual is still passing on its own genes to the next generation, albeit indirectly.

While altruism is well accepted, the existence of spiteful behaviors, which are costly to both the actor ( $c > 0$ ) and the recipient ( $b < 0$ ), has remained controversial. Spite can be predicted by Hamilton's rule if relatedness is sufficiently negative ( $r < 0$ ) so that  $rb - c > 0$ . Relatedness can take negative values, because it is in principle a regression coefficient: negative relatedness occurs when the actor is less related to the recipient than average (Hamilton 1970; Grafen 1985). Hamilton initially argued that negative relatedness would be nontrivial only in very small populations, and so spite would be of limited importance (Hamilton 1970, 1971, 1996; Wilson 1975; Knowlton and Parker 1979; Keller et al. 1994). In contrast, more recent work has argued that spite may, in fact, occur (Hurst 1991; Keller and Ross 1998; Foster et al. 2000, 2001; Gardner and West 2004a, 2004b, 2006b; Gardner et al. 2004; Lehmann et al. 2006). In particular, it has been suggested that local competition for resources can lead to sufficiently negative relatedness and hence selection for spiteful behaviors, even in large populations (Gardner and West 2004a, 2004b, 2006b; Gardner et al. 2004; Pen and West 2006). However, previous theory in this area has been based on very simple models. While these have been extremely useful for showing that spite could theoretically occur, it is not clear how well this body of theory applies more generally with con-

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sideration of realistic complications such as age or sex-structured populations, where different individuals vary in their reproductive values and hence cannot be considered as equivalent.

Here, we focus on a prime candidate for a spiteful behavior: the sterile soldier caste in polyembryonic parasitoid wasps (Gardner and West 2004a). In some (but not all) species belonging to the hymenopteran family Encyrtidae, a fraction of larvae develop precociously as soldiers (Cruz 1986; Strand 2003), giving up their own future reproduction in order to kill competitors, including opposite sex siblings, developing in the same host (Grbic et al. 1992; Giron et al. 2004). The unusual biology of these wasps, combined with the asymmetrical coefficients of relatedness produced by haplodiploid genetics, leads to conflicts between relatives over resource use and the proportion of offspring that are male (sex ratio); this offers some unique opportunities for testing social evolution theory. However, while there have been a number of elegant experimental studies, there has been confusion over the theoretical issues, with sterile soldiers having been variously referred to as selfish, altruistic, and spiteful (Cruz 1986; Godfray 1992; Grbic et al. 1992; Hardy 1995; Ode and Strand 1995; Ode and Hunter 2002; Donnell et al. 2004; Gardner and West 2004a, 2004b, 2006b; Giron and Strand 2004; Giron et al. 2004, forthcoming).

A potential role of spite has been suggested in polyembryonic wasps because they appear to provide the conditions necessary for it to evolve (Gardner and West 2004a, 2004b, 2006b). First, selection for spite is greatest when individuals have the capacity to discriminate between kin and preferentially direct spite toward individuals to which they are less related (Hamilton 1970). It has been shown that the soldier caste can do this, with a strong negative correlation between attack rates and relatedness (Giron and Strand 2004; Giron et al. 2004). The cue used to assess relatedness appears to be the extraembryonic membrane surrounding each larva during its development in their host. Attack rates correlated negatively with relatedness when the membrane was present (or transplanted) but not when it was removed (Giron and Strand 2004). Second, selection for spite is increased when there is strong competition for local resources (Gardner and West 2004b). This occurs in polyembryonic species because asexual proliferation produces multiple larvae, which can lead to severe competition for host resources (Strand 1989; Ode and Strand 1995; Ode and Hunter 2002).

We use the direct (neighbor-modulated) fitness approach of Taylor and Frank (1996; Frank 1997, 1998) to model the evolution of the sterile soldier caste in polyembryonic wasps. The advantage of this approach is that it provides a method for accounting for the social consequences of a behavior that does not make any a priori

assumptions about the form of selection on a trait (e.g., selfishness, altruism, spite). In particular, it does not use Hamilton's rule as the starting point for an analysis. Instead, the biological assumptions lead to a description of the action of selection that can be interpreted as a Hamilton's rule, and this can then be examined to determine whether it is consistent with altruism, spite, selfishness, or mutual benefit (fig. 1). Our specific aims are to (1) make testable predictions for how the production of sterile soldiers and wasp sex ratio (proportion male) should vary with key ecological parameters, (2) determine whether the biology of sterile reproductive soldiers is best explained by their role being defense against competitors or a means of mediating sex ratio conflict between siblings, (3) examine the extent to which sterile soldiers represent a spiteful trait, and (4) use our specific results to illustrate several general points about the evolution of spite.

## Models and Analyses

### *Basic Model*

Parasitoid wasps are insects whose larvae develop by feeding on the bodies of other arthropods, usually insects (Godfray 1994). Some parasitoid wasp species are polyembryonic, which means that multiple embryos develop from a single egg, giving rise to multiple genetically identical offspring. Our aim here is to develop a model of intermediate complexity for polyembryonic wasps that remains simple enough to address general points yet captures the essential features of a complex biology: the species on which our model is most directly based are *Copidosoma floridanum* (Ashmead) and other members of the hymenopteran family Encyrtidae (Strand and Grbic 1997; Strand 2003).

We assume a large patch-structured population with a single host on every patch. Each host is parasitized by a single mated female wasp, which lays one fertilized (diploid, female) egg and one unfertilized (haploid, male) egg into the host (we thus do not consider interactions between nonsibling clones following conspecific superparasitism; Giron and Strand 2004; Giron et al. 2004, forthcoming). Each egg then proliferates clonally to produce a large number of embryos of the same sex, so that there

		Effect on recipient	
		+	-
Effect on actor	+	Mutual benefit	Selfishness
	-	Altruism	Spite

**Figure 1:** Classification of social behaviors, after Hamilton (1964) and West et al. (forthcoming).

is a large collection of clonal female embryos and clonal male embryos. Competition for host resources ensues, and  $N_m$  adult males and  $N_f$  adult females emerge from the host upon its death (all notation is summarized in table 1). In order to keep the discussion of our model relatively simple, we assume that the number of emerging individuals, but

not their size, is influenced by competition for resources in the host. However, (a) our results could be interpreted in terms of the trade-off between size and number of individuals—by reinterpreting the quantities  $N_m$  and  $N_f$  as numbers of “reproductive units” rather than numbers of individuals—to give the same qualitative results and con-

**Table 1:** Summary of notation used in this article

Symbol	Definition
$N_f$	Number of adult females emerging from a focal host
$N_m$	Number of adult males emerging from a focal host
$d_f$	Premating dispersal rate of females
$d_m$	Premating dispersal rate of males
$F$	Probability of sibmating; $f = (1 - d_m)(1 - d_f)$
M	Mother
F	Father
S	Sister
B	Brother
$p_{ij}$	Consanguinity between individuals $i$ and $j$
$r_{ji}$	Relatedness of individual $j$ to individual $i$ , $p_{ij}/p_{ii}$
$w$	Fitness
$w_f$	Fitness of a focal female
$w'_f$	Fitness of the sister of a focal male
$w_m$	Fitness of a focal male
$w'_m$	Fitness of the brother of a focal female
$c_f$	Class reproductive value of females, 2/3
$c_m$	Class reproductive value of males, 1/3
$X$	Female soldier strategy; probability of a female developing as a soldier
$x$	Soldier strategy employed by a focal female
$x'$	Soldier strategy employed by the sisters of a focal male
$\bar{x}$	Average female soldier strategy
$x^*$	Continuously stable female soldier strategy
$G$	Genetic locus controlling female soldier strategy
$g$	Genic value of a random gene from locus $G$ in a focal individual
$g'$	Genic value of a random gene from locus $G$ in sister of a focal male
$\hat{g}$	Breeding value for phenotype $X$ at locus $G$ for focal female
$\hat{g}'$	Breeding value of phenotype $X$ at locus $G$ for sister of focal male
$Y$	Male soldier strategy; probability of a male developing as a soldier
$y$	Soldier strategy employed by a focal male
$y'$	Soldier strategy employed by the brothers of a focal female
$\bar{y}$	Average male soldier strategy
$y^*$	Continuously stable male soldier strategy
$H$	Genetic locus controlling male soldier strategy
$h$	Genic value of a random gene from locus $H$ in a focal individual
$h'$	Genic value of a random gene from locus $H$ in brother of a focal female
$\hat{h}$	Breeding value for phenotype $Y$ at locus $H$ for focal male
$\hat{h}'$	Breeding value for phenotype $Y$ at locus $H$ for brother of focal female
$z$	Sex ratio, the proportion of emerging adults that are male
$z_i^*$	Preferred sex ratio from the point of view of an individual $i$
$b$	Group benefit of altruistic soldier function
$k$	Shape parameter for soldier-mediated killing curve
$s$	Degree of soft selection at the level of the host
$n$	Number of extra males killed if a female develops as a soldier
$\rho_m$	Life-for-life relatedness of a male hostmate (brother) to a focal female
$\rho_f$	Life-for-life relatedness of a female hostmate (sister) to a focal female
$\bar{\rho}$	Life-for-life relatedness of the average hostmate to a focal female

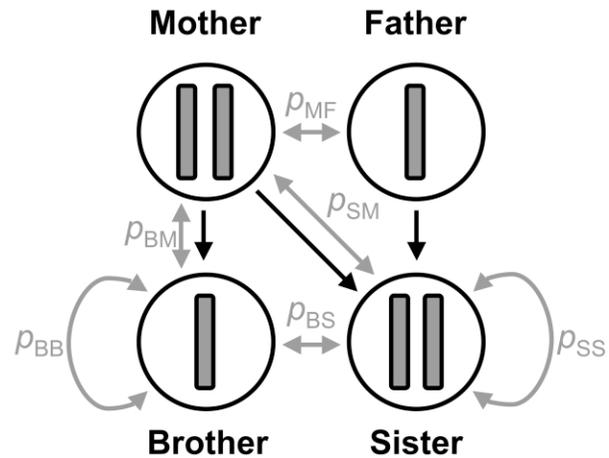
clusions of this analysis; and (b) when brood sizes are large, as is the case with polyembryonic species (see below), selection favors adjustment of the clutch size such that variation in body size will be negligible (Charnov and Downhower 1995; West et al. 2001; Guinnee et al., forthcoming).

We assume a very large number of emergents ( $N_r$ ,  $N_m \gg 1$ ), which is empirically supported (e.g., Ode and Strand 1995 report minimum brood sizes of approximately 600 for *C. floridanum*) and allows for a simple, deterministic analysis. A proportion  $d_m$  of males and a proportion  $d_f$  of females disperse to random patches elsewhere in the population, and the nondispersing individuals remain on their natal patch. Random within-patch mating ensues—so the frequency of sibmating is  $(1 - d_f)(1 - d_m)$ —followed by male death and dispersal of the mated females to colonize new patches. This allows us to vary the mating system between the extremes of complete inbreeding (complete local mate competition [LMC]; Hamilton 1967) to panmictic mating with no inbreeding. Polyembryonic wasp mating structures are thought to be at an intermediate state, with some, but not complete, inbreeding (i.e., partial LMC; Hardy 1994; Ode and Hunter 2002; Giron et al. 2004).

#### Genetical Associations

An important feature of this model is that it is “closed” so that relatedness and mate competition emerge from the model parameters rather than being specified explicitly (for a comparison of different approaches, see Gardner and West 2006a). This is helpful in two ways. First, it reduces the number of parameters required in the model, which leads to a simpler analysis. Second, relatedness and competition are not independent, so treating them as such could lead to potentially important biological effects being overlooked. Assuming that the system is at equilibrium, the above model provides enough information for us to determine the genetical associations between members of each family. There are four family members: mother (M), father (F), brother (B), and sister (S), where brother or sister denotes a single embryo before clonal proliferation. Figure 2 illustrates this family unit, the haplodiploid mode of inheritance, and several coefficients describing consanguinity between family members (the probability that two genes picked at random from homologous loci in the two individuals are identical by descent; calculated in the appendix). The coefficients of consanguinity combine to give kin selection coefficients of relatedness (see below).

It is important to be clear about what is denoted by a coefficient of relatedness, since relatedness between two individuals may not be the same in both directions (Grafen 1985). In general, we will describe the genetic similarity



**Figure 2:** Family unit (mother, father, brother, sister), with haplodiploid mode of inheritance. Coefficients of consanguinity are shown for mother and father ( $p_{MF}$ ), brother and sister ( $p_{BS}$ ), brother and brother ( $p_{BB}$ ), sister and sister ( $p_{SS}$ ), mother and brother ( $p_{BM}$ ), and mother and sister ( $p_{SM}$ ).

of an individual  $j$  to an individual  $i$  from the point of view of the individual  $i$  as “the relatedness of  $j$  to  $i$ ,” and we denote this  $r_{ji}$ . From the regression definition of relatedness, we can write  $r_{ji} = (p_j - p)/(p_i - p)$ , where a gene has been drawn from at random from  $i$ ,  $p_i$  is the probability of drawing the same allele from  $i$  in any further draw,  $p_j$  is the probability of drawing the same allele from  $j$ , and  $p$  is the frequency of the allele in the population (Grafen 1985). Because we will employ an evolutionary game theoretic approach in which we focus on the invasion success of a vanishingly rare allele, we can write  $r_{ji} \rightarrow p_{ij}/p_{ii}$  as  $p \rightarrow 0$ , where  $p_{ij}$  and  $p_{ii}$  are, respectively, the coefficients of consanguinity for the individuals  $i$  and  $j$  and for individual  $i$  to itself. We employ four coefficients of relatedness: the relatedness of (1) brother to sister,  $r_{BS} = p_{BS}/p_{SS}$ ; (2) sister to brother,  $r_{SB} = p_{BS}/p_{BB}$ ; (3) son to mother,  $r_{BM} = p_{BM}/p_{MM} = p_{BM}/p_{SS}$ ; and (4) daughter to mother,  $r_{SM} = p_{SM}/p_{MM} = p_{SM}/p_{SS}$ . (Note that the consanguinity of a mother to herself is the same as the consanguinity of any female to herself or of any female to any one of her clonal sisters, so  $p_{MM} = p_{SS}$ .) These relatedness coefficients are summarized in table 2.

#### Kin Selection in a Class-Structured Population

We pursue our kin selection analyses using the direct (neighbor-modulated) fitness approach described by Taylor and Frank (1996; Frank 1997, 1998). The direct fitness approach begins with an expression describing an individual’s total personal fitness as a function of its own behavior and the behaviors of its social partners, and it is

**Table 2:** Summary of coefficients of relatedness used in the kin selection analysis

Genealogical relationship	Relatedness coefficient	Consanguinity ratio	In terms of model parameters
Brother to sister	$r_{BS}$	$\frac{p_{BS}}{p_{SS}}$	$\frac{1}{2 - (1 - d_m)(1 - d_f)}$
		$\frac{p_{SS}}{p_{BB}}$	$\frac{1}{4 - 3(1 - d_m)(1 - d_f)}$
Sister to brother	$r_{SB}$	$\frac{p_{BS}}{p_{SS}}$	$\frac{1}{2 - (1 - d_m)(1 - d_f)}$
		$\frac{p_{BB}}{p_{SS}}$	$\frac{1}{4 - 3(1 - d_m)(1 - d_f)}$
Son to mother	$r_{BM}$	$\frac{p_{BM}}{p_{SS}}$	1
Daughter to mother	$r_{SM}$	$\frac{p_{SS}}{p_{SS}}$	1
		$\frac{p_{SM}}{p_{SS}}$	$\frac{1}{2 - (1 - d_m)(1 - d_f)}$

exactly equivalent to the more familiar inclusive fitness approach of Hamilton (1964; see Frank 1997, 1998; Taylor et al. 2006). For a class-structured population, fitness ( $w$ ) is derived by averaging over the fitness of individuals in each class, weighting by class reproductive value (Taylor and Frank 1996). These weightings allow for the possibility that different classes contribute differently to future generations (Fisher 1930; Price and Smith 1972). In the context of this model, we have

$$w = c_f w_f + c_m w_m, \tag{1}$$

where  $w_f$  and  $w_m$  are the fitness of a female and male individual, respectively, normalized so that the average fitness of a female and male are equal ( $\bar{w}_f = \bar{w}_m$ ), and  $c_f$  and  $c_m$  are the class reproductive values of females and males, respectively. As described by Price (1970) and derived explicitly by Taylor (1996), the class reproductive values appropriate for haplodiploidy are  $c_f = 2/3$  and  $c_m = 1/3$ , since the females make a genetic contribution to future generations that is twice as great as the contribution of the males. The fitness of a female embryo is given by the expected number of emerging adult females after clonal proliferation and development within the host:  $w_f = N_f$ . The fitness of a male embryo is given by expected mating success, which is determined by the number of emerging adult males and the ratio of females to males in the mating groups within which they compete:

$$w_m = N_m \left[ d_m \frac{\bar{N}_f}{\bar{N}_m} + (1 - d_m) \frac{(1 - d_f)N_f + d_f \bar{N}_f}{(1 - d_m)N_m + d_m \bar{N}_m} \right], \tag{2}$$

where  $\bar{N}_f$  and  $\bar{N}_m$  are the population averages of  $N_f$  and  $N_m$ , respectively. Note that, consistent with the normalization assumption for equation (1),  $\bar{w}_f = \bar{w}_m = \bar{N}_f$ .

## Results and Discussion

### *Conflict over the Sex Ratio*

It has been suggested that in polyembryonic wasps, there is a conflict over the sex ratio (proportion of male offspring) from the perspective of the mother, sons, and daughters and that this is important to the evolution of the sterile soldier caste (Grbic et al. 1992; Godfray 1994; Hardy 1994; Ode and Strand 1995; Ode and Hunter 2002; Giron et al. 2004, forthcoming; Corley et al. 2005). Crucial to this is the mating system and, in particular, the extent to which brothers compete for mates, some of which are their sisters. Local mate competition selects for female-biased sex ratios (Hamilton 1967). A female bias is favored because it reduces the competition among sons and provides more mates for each son (Taylor 1981). With maternal control of sex allocation, an additional bias is favored in haplodiploid species because inbreeding causes mothers to value their daughters more than their sons (Hamilton 1972; Frank 1985; Herre 1985).

Here, we examine the conflict over the sex ratio before adding in the complications that arise with the production of sterile soldiers. We assume that the total number of adult wasps emerging from a host is a constant,  $N = N_m + N_f$ , and that the sex ratio (proportion of offspring that are male) among the emergents is  $z = N_m/N$ . We then assume that different family members are in control of the sex ratio, and we determine the evolutionarily stable strategy (ESS; Maynard Smith and Price 1973), which may also be interpreted as the sex ratio preferred by that family member (see appendix for details). Although we will later focus on how sons and daughters can adjust the sex ratio through the production of soldiers, we also include the ESS sex ratio from the mother’s perspective for completeness and for comparison with previous theory (Werren and Hatcher 2000; Beukeboom et al. 2001; Pen 2006). We find that the ESS sex ratios for the sister ( $z_s^*$ ), brother ( $z_b^*$ ), and mother ( $z_m^*$ ) are, respectively,

$$z_s^* = \frac{(2 - d_m)d_m}{3 + d_f(1 - d_m) + (3 - d_m)d_m}, \quad (3)$$

$$z_b^* = \frac{[1 + 3d_f(1 - d_m) + 3d_m](2 - d_m)d_m}{3 - 3d_f^2(1 - d_m)^2 + d_f(1 - d_m)(2 - 3d_m^2) + d_m[4 + d_m(2 - 3d_m)]}, \quad (4)$$

$$z_m^* = \frac{[1 + d_f(1 - d_m) + d_m](2 - d_m)d_m}{3 - d_f^2(1 - d_m)^2 + 2d_m + d_f(1 - d_m)d_m^2 + d_m^3}. \quad (5)$$

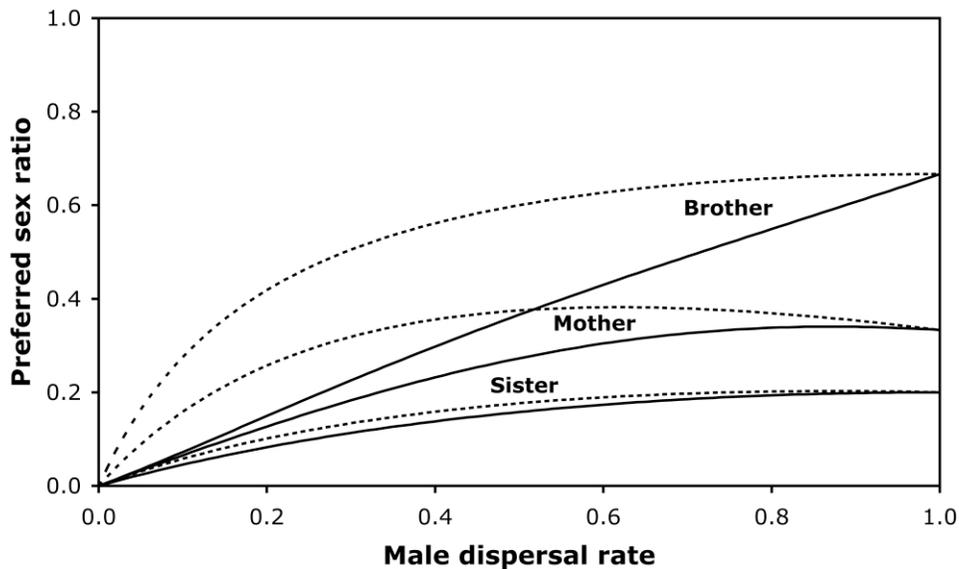
Dispersal influences the optimal sex ratio in two ways. First, male and female dispersal both impact on the various relatedness coefficients, which can be expressed as functions of the inbreeding coefficient  $f = (1 - d_m)(1 - d_f)$ . Second, the rate of male dispersal determines the intensity of local competition for mates. Numerical examples are given in figure 3. At one extreme, if all mating takes place between individuals from the same host and there is complete sibmating ( $d_m = d_f = 0$ ), the ESS from all perspectives will be to produce a sex ratio of 0, which is interpreted as producing the minimum numbers of sons to mate the daughters. This situation therefore leads to no intrafamilial conflict and agrees with previous theory (Hamilton 1967). As the rate of female or male dispersal before mating increases, it leads to lower levels of LMC, selecting for a less female-biased sex ratio (Taylor 1993). However, it also leads to conflict, with a different sex ratio being favored from the perspective of the mother, daughters, and sons (in agreement with previous verbal arguments; Godfray

1994; Hardy 1994; Ode and Hunter 2002). Although empirical testing of LMC can be facilitated by expressing the ESS sex ratio as a function of only inbreeding rate (Taylor 1993; Nee et al. 2002), this is not possible here, where we allow both sexes to disperse.

Daughters will favor a more female-biased sex ratio than their mothers or brothers because they are more related to their clonal sisters than to their brothers. Similarly, sons will favor a less biased sex ratio than their mother or sisters, because they are more related to their clonal brothers than to their sisters. As the opportunities for males to obtain mates elsewhere increase, this decreases the extent of LMC, favoring a less female-biased sex ratio and leading to an increased conflict. This could be tested by comparing sex ratios and soldier production/aggression across populations that differ in inbreeding rates.

#### *A General Model of Soldier Production and Function*

We now extend our model to allow for the production of sterile soldiers. In some polyembryonic species, there are distinct morphological castes where individuals from the same egg can develop through two alternate pathways. Some (usually most) individuals will develop as “reproductive larvae” that develop into adult wasps, provided that they survive resource competition in the host. In contrast, a minority of individuals develop as “precocious larvae” that possess enlarged mandibles, never moult, and



**Figure 3:** Preferred sex ratio,  $z^*$ , from the point of view of the brother, sister, and mother for a range of male pre-mating dispersal ( $0 \leq d_m \leq 1$ ). The solid lines are for no female pre-mating dispersal ( $d_f = 0$ ), and the dotted lines are for full female pre-mating dispersal ( $d_f = 1$ ). Note that pre-mating dispersal of males generates conflict of interest over sex ratio optima.

die when their reproductive siblings consume the host (Grbic et al. 1992; Donnell et al. 2004; Zhurov et al. 2004; Corley et al. 2005; Donnell and Strand 2006). Two classes of function have been proposed for these sterile soldiers. First, soldiers may provide a general benefit to their siblings by attacking the larvae of other parasitoid species (Cruz 1981; Strand et al. 1990; Harvey et al. 2000; Giron et al., forthcoming) or by physical maceration of host tissues to improve release of resources (Silvestri 1906). We term this the defense and facilitation hypothesis. Second, they may provide a weapon against relatives and other conspecifics in the sex ratio conflict. Specifically, female soldiers could kill males to produce a more female-biased sex ratio, and male soldiers could kill females to produce a less female-biased sex ratio (Godfray 1992; Hardy 1994; Ode and Hunter 2002; Giron et al., forthcoming). We term this the conflict hypothesis. In this section, we use our basic model to determine which of these hypotheses is most consistent with the observed distribution of sterile soldiers.

We describe the proportion of female embryos developing as soldiers as  $X$  and the proportion of male embryos developing as soldiers as  $Y$ . When referring to a focal female, we will denote the soldier strategy of this female as  $x$  and her brothers' soldier strategy as  $y'$ . When referring to a focal male, we will denote the soldier strategy of the male as  $y$  and his sisters' soldier strategy as  $x'$ . The population average strategies for both sexes are  $\bar{x}$  and  $\bar{y}$  for females and males, respectively. Soldier function is expected to impact both the number of adults ( $N$ ) emerging from the host and the sex ratio ( $z$ ) among these emergents. We describe this dependency in a very general way by making explicit that both  $N$  and  $z$  are functions of male and female allocation to the soldier caste. In the appendix, we show that the direction of sex bias in soldier production has a simple relationship to the form of these generalized functions. We do this by (1) assuming that the sexes currently allocate equally to soldier production, (2) setting the female trait to its ESS value, and (3) determining the direction of evolution in the male trait ( $y$ ) under the action of selection. If selection acts to increase the male allocation to soldier production at this point, then males are predicted to have a greater ESS production of soldiers than females. Conversely, if selection acts to decrease the male allocation to soldier production, then the male soldier production ESS is predicted to be lower than that for females.

We use the above approach to assess the validity of the two competing hypotheses for soldier function. In particular, under the defense and facilitation hypothesis, we expect increasing soldier production to be associated with an increase in the number of adult wasps emerging from the parasitized host (at least when this defense and facilitation is helpful). Conversely, under the conflict hypothesis,

we expect increasing soldier production to be associated with a decrease in the number of adult wasps emerging from the host. We find that if the function of soldiers is predominantly one of defense and facilitation, then it is the males that are expected to allocate more toward soldier production. Results obtained from an illustrative model of defense and facilitation function support this prediction and additionally show that allocation to soldier function should increase as the benefit soldiers bring to their siblings increases (fig. 4, *left column*). If the function of the soldiers is primarily to manipulate the sex ratio in that sex's favor, then it is the females that are predicted to allocate more to the production of the soldier caste. Again, this is supported by an example model of conflict function, which also suggests that soldier production should increase with the degree of soft selection (the intensity of resource competition; Wallace 1968; Gardner and West 2006a, 2006b) at the level of the host (fig. 4, *middle and right columns*). Both hypotheses predict that any sex ratio bias will be in favor of females (fig. 4). For simplicity, we have assumed a single foundress of the focal species ovipositing in each parasitized host; hence, our model does not address interactions between unrelated conspecifics.

In *Copidosoma floridanum* and congeners, the sterile soldiers are predominantly or even exclusively females (Doutt 1947; Grbic et al. 1992; Ode and Strand 1995; Keasar et al. 2006; Giron et al., forthcoming; for *Copidosoma sosares*, P. J. Ode and M. R. Strand, personal communication), suggesting that the primary function of soldiers (at least in mixed-sex full-sibling broods) is sex ratio manipulation (conflict) and not defense and facilitation. This conclusion is further supported by empirical observations that female soldiers preferentially kill the males when both sexes are developing in a host (Grbic et al. 1992; Giron et al. 2004, forthcoming). Males appear to try to avoid attack by "hiding" in the fat tissues of the host abdomen (Grbic et al. 1992), but soldier action still leads to female-biased sex ratios as extreme as 10% male (Strand 1989; Grbic et al. 1992; Walter and Clarke 1992; Ode and Strand 1995).

Our model predicts how the pattern of soldier production could vary across species. For example, in species where most broods are single sex, there is no sex ratio conflict, and so soldiers could be favored in both sexes for defense purposes. Comparative work examining how soldier production varies with the oviposition behavior of females and species ecology would be extremely useful. Furthermore, even in species such as *C. floridanum*, soldiers may have multiple functions. Recent empirical investigations do lend support to our prediction that the primary function of soldiers is to mediate intraspecific conflict (Giron et al., forthcoming). However, these studies

**Figure 4:** Impact of mating system on male and female soldier production and the resulting sex ratio among emerging wasps for three different models of soldier function: defense and facilitation function; conflict function, with no self-restraint; and conflict function, with self restraint (where individuals choose not to develop at all in order to free up resources for hostmates). For simplicity, we assume no dispersal of females before mating ( $d_f = 0$ ) and allow male dispersal to vary between the extremes of local mate competition ( $d_m = 0$ ) to panmixis ( $d_m = 1$ ). *Top row*, male soldier production with defense and facilitation function (*left*; with varying group benefit  $b$ ), conflict function with no self-restraint (*middle*; with varying soft selection  $s$ ), and conflict function with self-restraint (*right*; with varying soft selection  $s$ ; dashed lines indicate the degree of self-restraint in terms of the proportion of males lost). *Middle row*, female soldier production with defense and facilitation function (*left*; with varying group benefit  $b$ ), conflict function with no self-restraint (*middle*; with varying soft selection  $s$ ), and conflict function with self-restraint (*right*; with varying soft selection  $s$ ). *Bottom row*, sex ratio among emergents with defense and facilitation function (*left*; with varying group benefit  $b$ ), conflict function with no self-restraint (*middle*; with varying soft selection  $s$ ), and conflict function with self-restraint (*right*; with varying soft selection  $s$ ). The key qualitative result is that the defense and facilitation hypothesis for soldier function leads to the prediction that soldiers will be predominantly male and, conversely, that the conflict hypothesis leads to the prediction that soldiers will be predominantly female.

have also shown that two morphologically distinguishable soldier types are produced during the course of clone development, with the earliest-produced soldiers specializing toward intraspecific conflict resolution and the later-produced soldiers being more involved in defense from interspecific competitors (Giron et al., forthcoming).

Alternative possibilities have been suggested to explain sex-biased soldier production. Doutt (1947) suggested that the haploid genome of males could be responsible for sex

differences in *Copidosoma* development. However, male soldiers do exist, so it is reasonable to assume that the proportions of embryos of each sex developing as sterile soldiers is unconstrained by ploidy. P. Nonacs (personal communication) has suggested that soldier-mediated killing could be directed toward poor-quality mutated individuals in an effort to remove deleterious mutations from the brood. However, (a) the benefit derived from such a “quality control” function is likely to be orders of mag-

nitude lower than the direct selection opposing sterility; and (b) this mutational elimination would benefit the whole brood, which could select for a male soldier bias, as with the defense and facilitation hypothesis.

### *Spiteful and Altruistic Hamilton's Rules*

Setting the predictions of our general model of soldier function alongside empirical observations of sex bias in soldier production, we have found in favor of the hypothesis that soldiers in mixed-sex, full-sibling broods of *C. floridanum* and related species have a primarily conflict-related function and, against the hypothesis, that they are primarily engaged in defense and facilitation activities. In this section, we conceptualize this result in terms of the general classification of social behaviors (fig. 1) and Hamilton's rule. In particular, we determine whether soldier function can be regarded as a spiteful, altruistic, or other form of trait.

It is instructive to restrict attention to a special case of our conflict model (described in the appendix) and examine the evolution of female soldier production when there is complete male premating dispersal ( $d_m = 1$ ) and males are not producing soldiers ( $y = 0$ ). Here, a condition for females to be selected to increase their allocation to soldier production is

$$-n\rho_m + s(n+1)\bar{\rho} - \rho_f > 0, \quad (6)$$

where  $n = k\bar{x}^{k-1}$  is the number of extra male hostmates (brothers) killed if the focal female develops as a soldier (the parameter  $k$  describes how soldier production translates into killing of the opposite sex, as described in the appendix);  $\rho_m = (\bar{N}_f/\bar{N}_m)c_m r_{BS}$  is the "life-for-life" relatedness (Hamilton 1972) of a brother to the focal female, being the product of the genetic relatedness ( $r_{BS}$ ) of brother to sister multiplied by the reproductive value of the brother,  $(\bar{N}_f/\bar{N}_m)c_m$ ;  $\rho_f = c_f$  is the life-for-life relatedness of a female hostmate (sister) to the focal female, being the product of their genetic relatedness ( $r_{SS} = 1$ ) and the reproductive value of the sister ( $c_f$ ); and  $\bar{\rho} = z\rho_m + (1-z)\rho_f$  is the life-for-life relatedness of the average hostmate to the focal female.

This can be interpreted as a three-party Hamilton's rule, with the net inclusive fitness effect if the female develops as a soldier summarized on the left-hand side of inequality (6) being the sum of the inclusive fitness decrement due to the killing of an extra  $n$  brothers ( $-n\rho_m$ ), the inclusive fitness decrement due to the loss of the female's own future reproduction ( $-\rho_f$ ), and the inclusive fitness increment due to the freeing up of a proportion  $s$  of these  $n+1$  individuals' resources for use by other hostmates ( $+s[n+1]\bar{\rho}$ ). One possible interpretation of this behavior is

that of "Wilsonian spite" (Wilson 1975), which is favored because of benefits received by a positively related third party (Foster et al. 2001) and which may also be thought of as "indirect altruism." An advantage of equation (6) is that relatedness is given by simple life-for-life measures, which can be understood by nonspecialists. A disadvantage is that it is difficult to conceptualize such a three-party Hamilton's rule in terms of the classic two-party classification (fig. 1), and so it is necessary to invoke a new class of behavior, such as indirect altruism.

We can rearrange equation (6) into a spiteful two-party Hamilton's rule by measuring relatedness of victims relative to competitors. Relatedness describes the genetic similarity of two individuals relative to the average genetic similarity between individuals within a reference population (Grafen 1985; Frank 1998). Consequently, provided all fitness effects are accounted for, then the scale at which relatedness is measured is a matter of preference (Queller 1994; West et al. 2002; Gardner and West 2004b; Lehmann et al. 2006). Queller (1994; see also Kelly 1994) showed that a natural measure of relatedness was to measure genetic similarity at the level at which competition occurs, the "economic neighborhood." Using this approach, Gardner et al. (2004; Gardner and West 2004b) showed that behaviors such as chemical warfare in microbes could be encapsulated by a spiteful two-party Hamilton's rule. Using a similar approach here, we can rearrange equation (6) to give:

$$\frac{\rho_m - s\bar{\rho}}{\rho_f - s\bar{\rho}}(-n) > 1. \quad (7)$$

Here we have the spiteful Hamilton's rule  $Rb > c$ , where  $b = -n$  is the negative benefit inflicted by the female against her victims;  $c = 1$  is the cost of the female's sacrifice of her own future reproductive success; and  $R = (\rho_m - s\bar{\rho})/(\rho_f - s\bar{\rho})$  is the coefficient of relatedness of the focal female to her brothers, measured relative to the average competitor,  $s\bar{\rho}$  (since a proportion  $s$  of competition is within host and hostmates are valued at  $\bar{\rho}$ , then the average competitor is valued at  $s\bar{\rho}$ ; Gardner and West 2006a). Because brothers are valued less than sisters ( $\rho_m < \rho_f$ ) and therefore less than the average hostmate ( $\rho_m < \bar{\rho}$ ), then provided that competition is sufficiently localized at the level of the host, brothers may be valued less than the average competitor ( $\rho_m < s\bar{\rho}$ ), giving a negative relatedness ( $R < 0$ ). This shows that it is also possible to interpret soldier production as spiteful, supporting the previous conclusion from idealized, simple models that examples of Wilsonian spite can also be interpreted as Hamiltonian spite (Gardner and West 2004a, 2006b; Lehmann et al. 2006).

Alternatively, we can also rearrange equation (6) into a two-party Hamilton's rule with an altruistic interpretation. Lehmann et al. (2006) showed that this can be done by measuring relatedness relative to the victims of the harming behavior. Applying this manipulation obtains

$$\frac{\bar{s}\bar{\rho} - \rho_m}{\rho_f - \rho_m}(n + 1) > 1. \quad (8)$$

The interpretation is that the above condition is an altruistic Hamilton's rule of the form  $Rb > c$ , where  $b = n + 1 > 0$  is the benefit to competitors due to soldier-mediated killing;  $c = 1 > 0$  is the personal cost of sterility for the soldier; and  $R = (\bar{s}\bar{\rho} - \rho_m)/(\rho_f - \rho_m)$  is the value of the average competitor, who benefits from the relaxation of competition that occurs in the wake of soldier-mediated killing, expressed relative to the value of a brother. In this way, we can switch from a spiteful to an altruistic interpretation of the soldier behavior. Both two-party Hamilton's rules and associated interpretations are mathematically equivalent and equally valid. However, the spite interpretation may be more natural in that it does not require quite the same stretching of the relatedness concept that is needed for the altruism interpretation. Relatedness, as a regression measure, should properly describe associations between individuals according to their nonindependent deviations from an average value. Thus, it should be possible to make a statement to the effect that the average relatedness is zero. There is some freedom in the choice of which average value to use, whether it be the average for a global population or among a much smaller neighborhood of resource competition. While the relatedness required for the spite interpretation can be easily understood in these terms (it is relatedness measured at the level of the economic neighborhood), it is more difficult to find a natural interpretation for the relatedness coefficient required for the altruism interpretation, which measures all relatednesses relative to one's brothers. We stress that the different ways in which one can combine the effects of relatedness, reproductive value, and competition into simple Hamilton's rule forms are of interest simply as conceptual aids that help one interpret mathematical results. For the purposes of deriving these results from a mathematical model, it will usually be simpler to use a direct fitness approach that keeps relatedness, reproductive value, and competition separate (Taylor and Frank 1996; Frank 1998; Wild and Taylor 2006; Taylor et al., forthcoming).

### Conclusions

Our model predicts that the sterile soldiers found in polyembryonic wasps should be predominantly males if their

role is to defend against other parasitoid species or to provide other benefits for the brood and predominantly female if their role is to mediate sex ratio conflict between males and females. Our model also predicts that sex ratio conflicts between male and female siblings in mixed-sex broods will occur when mating is not exclusively local. Consequently, the fact that soldiers are predominantly female in *Copidosoma floridanum* and related polyembryonic parasitoids suggests their main role is to mediate conflict over the sex ratio. This could be further tested by examining how soldier production and aggression varies across populations and species. The behavioral distinction between early- and late-produced soldier larvae also warrants further attention. We have also shown that the production of the sterile soldier caste can be classed as a spiteful trait but that this is a semantic choice. The equations can be rearranged to forms that could be equally termed indirect altruism, altruism, Wilsonian spite, or Hamiltonian spite. All are correct, and the choice is merely a matter of preference or relative use for the purpose at hand.

This raises the general point that at different times it can be useful to lump ideas together or to split them up (Maynard Smith 1976). Neither approach is more correct; they are merely useful at different times. If our aim is to provide a general theoretical overview, then it is useful to lump concepts together. Altruism and spite are both favored because they lead to an increase in inclusive fitness (Hamilton 1970). Furthermore, behaviors that can be classified as spite can equally be termed altruism, indirect altruism, Hamiltonian spite, or Wilsonian spite (Gardner and West 2004b, 2006b; Lehmann et al. 2006); appreciating this will prevent fruitless debate. More generally, the value of lumping or combining concepts has been elegantly demonstrated by Frank's (1998) unification of social evolution theory. In contrast, if our aim is to classify real behaviors and stimulate empirical research, then it can be useful to distinguish between altruism (e.g., directly helping) and spite (e.g., directly harming). First, although it is possible to rearrange a spiteful Hamilton's rule to give an altruistic form, this requires the recipient of the behavior to be defined indirectly. So, for the example considered in this article, the recipients of soldier-mediated killing are not the wasp larvae attacked but the other unattacked larvae. While this can be done, it can be useful to retain the recipient of the behavior as the recipient in Hamilton's rule. For example, while it would be possible to rearrange Hamilton's rule for a (cooperative or helpful) altruistic behavior into a spiteful form, we would not expect this to be useful or for altruistic helping to be referred to as spite or indirect spite (on the basis that helping relatives is beneficial because it increases competition for nonrelatives; Lehmann et al. 2006). In addition, as discussed in

“Results and Discussion,” defining the recipient to obtain a spiteful interpretation can lead to a more natural interpretation of relatedness.

More importantly, there are biologically interesting differences between behaviors that are altruistic (helping) and spiteful (harming), defined according to those conspecifics that are the most direct recipients of the behavior. For example, (a) local competition for resources between a small number of lineages selects for spite but against altruism (West et al. 2002; Gardner and West 2004b, 2006a); (b) spiteful behaviors are often predicted to show a domed relationship with average relatedness in a patch (Gardner and West 2004b; Gardner et al. 2004), whereas altruistic behaviors are usually predicted to show a positive correlation with the average relatedness in a patch (Frank 1998); and (c) a large number of situations can select for altruism directed indiscriminately toward all neighbors, since those neighbors tend to be relatives (West et al. 2002), whereas it is extremely hard to find situations that select for indiscriminate spite (Pen and West 2006). Appreciating these differences aids the classification of real behaviors and separates cases where different predictions arise.

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#### APPENDIX

##### *Genetical Associations*

Here we derive expressions for various coefficients of consanguinity between (and within) family members. At equilibrium, the consanguinity between mating partners is simply that of opposite sex siblings ( $p_{BS}$ ) weighted by the frequency of inbreeding  $(1 - d_m)(1 - d_f)$ :  $p_{MF} = (1 - d_m)(1 - d_f)p_{BS}$ . The consanguinity of a brother and sister is given by that of the mother to herself ( $p_{SS}$ ) weighted by the probability that both her son and daughter derived the focal genes from her (1/2), plus the consanguinity between the mother and her mating partner ( $p_{MF}$ ) weighted by the probability that the son derived his focal gene from his mother and the daughter derived her focal gene from her father (1/2):  $p_{BS} = (p_{SS} + p_{MF})/2$ . The consanguinity of a female to herself (or to a clonal sister) is the probability that the same gene is drawn from her twice (1/2), plus the probability that the maternal and paternal gene are drawn (1/2) weighted by the consanguinity between her parents ( $p_{MF}$ ):  $p_{SS} = (1 + p_{MF})/2$ . Starting with  $p_{BS} = (p_{SS} + p_{MF})/2$ , we substitute

in our expression for  $p_{SS}$ , giving  $p_{BS} = [(1 + p_{MF})/2 + p_{MF}]/2 = (1 + 3p_{MF})/4$ . Also, since  $p_{MF} = (1 - d_m)(1 - d_f)p_{BS}$ , we can rewrite this as  $p_{BS} = [1 + 3(1 - d_m)(1 - d_f)p_{BS}]/4$ , which rearranges to give  $p_{BS} = 1/[4 - 3(1 - d_m)(1 - d_f)]$ , so we can express the consanguinity between a brother and sister in terms of male and female dispersal rates. Having obtained this, we can find  $p_{MF} = (1 - d_m)(1 - d_f)p_{BS} = (1 - d_m)(1 - d_f)/[4 - 3(1 - d_m)(1 - d_f)]$ , and  $p_{SS} = (1 + p_{MF})/2 = [2 - (1 - d_m)(1 - d_f)]/[4 - 3(1 - d_m)(1 - d_f)]$ . Since males contain a single gene at each locus and brothers are clonal, the consanguinity of a male to himself or to a brother is  $p_{BB} = 1$ . Since the gene in the male is a random draw from his mother, the consanguinity of a mother and son is simply the consanguinity of the mother to herself:  $p_{BM} = p_{SS} = [2 - (1 - d_m)(1 - d_f)]/[4 - 3(1 - d_m)(1 - d_f)]$ . Finally, since a gene in a daughter is with equal probability a draw from a mother or the mating partner of that mother, the consanguinity of a mother and daughter is  $p_{SM} = p_{SS}/2 + p_{MF}/2 = 1/[4 - 3(1 - d_m)(1 - d_f)]$ . Having described these coefficients of consanguinity, we can express kin selection coefficients of relatedness in terms of the model parameters ( $d_m$  and  $d_f$ ), and these are summarized in table 2.

##### *Kin Selection in a Class-Structured Population*

Consider genetic variation at a locus  $G$  controlling a phenotypic trait  $X$  expressed by females only. If  $g$  is the genic value of a gene drawn from locus  $G$  at random from the population, then the action of natural selection is to increase the average genic value when  $dw/dg > 0$ . Associations with fitness are due to (1) the focal individual's genic value being associated with her own phenotype ( $x$ ) when she is female, and hence the effect of this phenotype on her direct fitness; and (2) the focal individual's genic value being associated with the phenotype of his sisters ( $x'$ ) when he is male, and hence the effect of the sisters' phenotype on his direct fitness. Following the procedure outlined by Taylor and Frank (1996), we may write

$$\frac{dw}{dg} = c_f \frac{dw_f}{dg} + c_m \frac{dw_m}{dg}. \quad (A1)$$

We now make explicit the link between genotype and phenotype by describing an individual's genetic breeding value for the phenotype as the average of the genic values for that individual. We denote this  $\hat{g}$  for the focal individual and  $\hat{g}'$  for the focal individual's sibling. Expanding the derivatives in equation (A1) according to the chain rule, we have

$$\frac{dw}{dg} = c_f \frac{\partial w_f}{\partial x} \frac{\partial x}{\partial \hat{g}} \frac{d\hat{g}}{dg} + c_m \frac{\partial w_m}{\partial x'} \frac{\partial x'}{\partial \hat{g}'} \frac{d\hat{g}'}{dg}. \quad (\text{A2})$$

Assuming that the breeding value maps to phenotypic trait in the same way for all females, we have  $\partial x'/\partial \hat{g}' = \partial x/\partial \hat{g}$ . We may also replace the derivatives of breeding value with respect to genic value with coefficients of consanguinity:  $d\hat{g}/dg = p_{SS}$  and  $d\hat{g}'/dg = p_{BS}$ . Having made these substitutions, we may write

$$\frac{dw}{dg} \propto c_f \frac{\partial w_f}{\partial x} + c_m \frac{\partial w_m}{\partial x'} r_{BS}. \quad (\text{A3})$$

The condition for increase is when the right-hand side (RHS) of expression (A3) is positive, yielding a Hamilton's rule (Hamilton 1963, 1964, 1970). We assume a positive association between breeding value and phenotype in the appropriate sex ( $\partial x/\partial \hat{g} = \partial x'/\partial \hat{g}' > 0$ ) and also vanishing variation in the trait about its population average value (so that eq. [6] is evaluated at  $x = x' = \bar{x}$ , and selection is sufficiently weak for us to use relatedness coefficients calculated in a neutral population). If  $\bar{x} = x^*$  is an evolutionarily stable strategy (ESS; Maynard Smith and Price 1973), then the RHS of equation (A3) is equal to 0 when evaluated at this point. Convergence stability (i.e., "attainability") requires that the RHS is positive for  $\bar{x} = x^* - \delta x$  and negative for  $\bar{x} = x^* + \delta x$ , where  $\delta x$  is a vanishingly small positive quantity (Eshel and Motro 1981; Taylor 1996). A strategy that is simultaneously evolutionarily and convergence stable is described as a continuously stable strategy (CSS; Eshel 1983; Christiansen 1991). It is such a strategy that is of interest to us because it is expected to both evolve and also be retained in natural populations, and thus it represents our expectation of the endpoint of the evolutionary process. Taking the perspective of a female actor who expresses phenotype  $x$  and switching  $\partial w_m/\partial x'$  (the impact of the sister's phenotype on a focal male's fitness) with  $\partial w'_m/\partial x$  (the impact of a focal female's phenotype on her brother's fitness), then from expression (A3), the CSS is the strategy  $x = x^*$  that, holding all other behavior fixed, maximizes the quantity  $c_f w_f + c_m w'_m r_{BS}$ , that is, Hamilton's (1964) inclusive fitness. This view provides a justification for using the analogy of agency (Grafen 2003) and associated intentional language (altruism, spite, conflict) such that the phenotype  $x^*$  can be regarded as the optimum, or preferred, strategy that a female should employ in order to maximize her inclusive fitness.

Similarly, for the males, we may describe a locus  $H$  that controls a male-limited trait  $Y$  that affects the direct fitness of the bearer and his sister. Denoting the genic value of a male  $h$ , we may employ the same argument to derive a condition for increase:

$$\frac{dw}{dh} \propto c_f \frac{\partial w_f}{\partial y'} r_{SB} + c_m \frac{\partial w_m}{\partial y}, \quad (\text{A4})$$

where  $y$  and  $y'$  are, respectively, the phenotypes of a focal male and the brother of a focal female. As with the sister, we may define a CSS  $y^*$  that sets the RHS of expression (A4) equal to 0 and can be regarded as the preferred strategy of the brother.

### Conflict over the Sex Ratio

Under the assumption that the number of adults emerging from each host is a constant  $N$  and the sex ratio among these emerging adults is a variable  $z$ , then we can write  $N_f = N(1 - z)$  and  $N_m = Nz$ , and  $\bar{N}_f = N(1 - \bar{z})$  and  $\bar{N}_m = N\bar{z}$ , where  $\bar{z}$  is the population average of  $z$ . By analogy to expression (A3), if we allow the sister to have complete control over sex allocation, we may define her preferred sex ratio  $z_s^*$  as satisfying

$$\left. \frac{dw}{dz} \right|_{z=\bar{z}=z_s^*} = c_f \frac{\partial w_f}{\partial z} + c_m \frac{\partial w_m}{\partial z} r_{BS} = 0. \quad (\text{A5})$$

Solving this obtains the sex ratio preferred by sisters, expression (3). If the brother has full control over the sex ratio, then his preferred sex ratio  $z_b^*$  satisfies

$$\left. \frac{dw}{dz} \right|_{z=\bar{z}=z_b^*} = c_f \frac{\partial w_f}{\partial z} r_{SB} + c_m \frac{\partial w_m}{\partial z} = 0. \quad (\text{A6})$$

Solving this obtains the sex ratio preferred by brothers, expression (4). Following the same procedure, we may define a condition for the mother's preferred sex ratio  $z_M^*$  as

$$\left. \frac{dw}{dz} \right|_{z=\bar{z}=z_M^*} = c_f \frac{\partial w_f}{\partial z} r_{SM} + c_m \frac{\partial w_m}{\partial z} r_{BM} = 0. \quad (\text{A7})$$

Solving this obtains expression (5).

### A General Model of Soldier Production and Function

We define generalized functions  $N = N(X, Y)$  and  $z = z(X, Y)$ , where  $X = x$  and  $Y = y'$  if the focal individual is female and  $X = x'$  and  $Y = y$  if the focal individual is male. Thus, we may write  $N_f = N(X, Y)(1 - z(X, Y))$  and  $N_m = N(X, Y)z(X, Y)$ . Substituting these into expression (A3) and assuming  $\bar{x} = \bar{y}$ , the marginal fitness for the female trait is

$$\begin{aligned} \frac{dw}{dg} &\propto c_f \left[ \frac{\partial N}{\partial x} (1-z) - N \frac{\partial z}{\partial x} \right] \\ &+ c_m \left\{ (1-d_m)(1-d_f) \left[ \frac{\partial N}{\partial x} (1-z) - N \frac{\partial z}{\partial x} \right] \right. \\ &\left. + [1 - (1-d_m)^2] \left( \frac{\partial N}{\partial x} z + N \frac{\partial z}{\partial x} \right) \right\} r_{BS}, \end{aligned} \quad (\text{A8})$$

where the partial derivatives are evaluated at  $x = \bar{x} = y' = \bar{y}$ . Similarly, we may write the marginal fitness for the male trait with reference to expression (A4):

$$\begin{aligned} \frac{dw}{dh} &\propto c_f \left[ \frac{\partial N}{\partial y} (1-z) - N \frac{\partial z}{\partial y} \right] r_{SB} \\ &+ c_m \left\{ (1-d_m)(1-d_f) \left[ \frac{\partial N}{\partial y} (1-z) - N \frac{\partial z}{\partial y} \right] \right. \\ &\left. + [1 - (1-d_m)^2] \left( \frac{\partial N}{\partial y} z + N \frac{\partial z}{\partial y} \right) \right\}, \end{aligned} \quad (\text{A9})$$

where the partial derivatives are evaluated at  $x' = \bar{x} = y = \bar{y}$ . Since both sexes are allocating equally to soldier production, the impact of increasing soldier production on total number of emerging adults is the same for both sexes, so  $\partial N/\partial x = \partial N/\partial y$ . Similarly, the impact on the sex ratio is equal in magnitude and opposite in direction, so we may write  $\partial z/\partial y = -\partial z/\partial x$ . Making these substitutions into expression (A8) and setting the female trait to equilibrium ( $dw/dg = 0$ ), we may solve for an explicit expression for  $\partial z/\partial x$ . Now, we may make these substitutions into expression (A9) to determine the direction of selection on the male trait when the female trait is at equilibrium, and this obtains

$$\frac{dw}{dh} \propto \frac{\frac{\partial N}{\partial x} c_f^2 r_{SB} + c_m^2 \phi [1 - d_f(1-d_m) + d_m(1-d_m)] r_{BS} + c_f c_m (1-d_m)(1-d_f)(1+r_{BS}r_{SB})}{c_f + c_m \phi r_{BS}}, \quad (\text{A10})$$

where  $\phi = [1 - d_f(1-d_m) - (3-d_m)d_m]$ . Substituting in the expressions for  $c_f$ ,  $c_m$ ,  $r_{BS}$ , and  $r_{SB}$ , we find that the RHS of expression (A10) always takes the same sign as  $\partial N/\partial x$ . Hence, when soldier production increases the output of adult wasps from the host ( $\partial N/\partial x = \partial N/\partial y > 0$ ), we predict male-biased soldier production ( $y^* > x^*$ ); conversely, when increase in soldier production leads to a decline in the output of adults from the host ( $\partial N/\partial x =$

$\partial N/\partial y < 0$ ), we predict female-biased soldier production ( $x^* > y^*$ ).

### Defense and Facilitation Hypothesis

As a simple illustration of the defense and facilitation hypothesis, we now assume that the total number of embryos surviving resource competition increases linearly with increasing proportion of embryos developing as soldiers, and those survivors that do not develop as soldiers emerge as adults; hence,

$$N \propto \left( 1 - b + b \frac{x+y}{2} \right) \left( 1 - \frac{x+y}{2} \right). \quad (\text{A11})$$

Here, the parameter  $b$  controls the relative increase in the number of embryos surviving resource competition due to soldier function. For sufficiently large  $b$ , soldier production increases the output of adult wasps from the host and thus satisfies  $\partial N/\partial x, \partial N/\partial y > 0$ . The sex ratio is the proportion of males among the nonsoldier embryos; that is,

$$z = \frac{1-y}{2-x-y}. \quad (\text{A12})$$

Substituting these functions into our marginal fitness expressions, we may determine the ESS  $x^*$  and  $y^*$ . Numerical examples of soldier production by both sexes, plus the resulting sex ratio, are given in figure 3 (*left column*).

### Conflict Hypothesis

We consider a simple model of the conflict hypothesis of soldier function. We assume that the proportion of nonsoldier males killed by female soldiers is given by  $x^k$ , where  $0 \leq k \leq 1$ ; in other words, this increases from none of the males to all of the nonsoldier males as the proportion of females developing as soldiers increases from 0 to 1, and there are diminishing returns on the killing of males. Similarly, the proportion of nonsoldier females killed by male soldiers is  $y^k$ . Then the proportion of males surviving (i.e., not becoming soldiers and not killed by soldiers) is  $(1-y)(1-x^k)$  and the proportion of surviving females is  $(1-x)(1-y^k)$ . We assume that the total number of emerging adults is given by a power function of the number of survivors, and hence

$$N \propto \left[ \frac{(1-x)(1-y^k) + (1-y)(1-x^k)}{2} \right]^{1-s}, \quad (\text{A13})$$

where  $0 \leq s \leq 1$  describes the degree of soft selection at

the level of the host. In the extreme of hard selection ( $s = 0$ ), then the number of emergents is proportional to the number of surviving embryos, and in the extreme of soft selection ( $s = 1$ ), the number of emerging adults is constant with respect to the degree of soldier action within the host. Assuming that emerging adults reflect the sex ratio among the surviving embryos, we also have

$$z = \frac{(1-y)(1-x^k)}{(1-y)(1-x^k) + (1-x)(1-y^k)}. \quad (\text{A14})$$

Substituting these expressions into our marginal fitness functions, we can perform an evolutionary stability analysis. Numerical examples of soldier production by both sexes, plus the resulting sex ratio, are given in figure 4 (*middle column*). An extension to this model that allows for voluntary limitation in the proliferation of male embryos in order to save resources for female embryos is also pursued. Allowing this growth limitation to evolve results allows for more extreme sex ratio bias, but otherwise the general qualitative results are not affected (fig. 4, *right column*).

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