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Theory of genomic imprinting conflict in social insects

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Abstract

Background: Genomic imprinting refers to the differential expression of genes inherited from the mother and father (matrigenes and patrigenes). The kinship theory of genomic imprinting treats parent-specific gene expression as products of within-genome conflict. Specifically, matrigenes and patrigenes will be in conflict over treatment of relatives to which they are differently related. Haplodiploid females have many such relatives, and social insects have many contexts in which they affect relatives, so haplodiploid social insects are prime candidates for tests of the kinship theory of imprinting.

Results: Matrigenic and patrigenic relatednesses are derived for individuals affected in a variety of contexts, including queen competition, sex ratio, worker laying of male eggs and policing, colony fission, and adoption of new queens. Numerous predictions emerge for what contexts should elicit imprinting, which individuals and tissues will show it, and the direction of imprinting effects. The predictions often vary for different genetic structures (varying queen and mate number) and often contrast with predictions for diploids.

Conclusion: Because the contexts differ from the normal imprinting case, and because nothing is currently known about imprinting in social insects, these predictions can serve as a strong *a priori* test of the kinship theory of imprinting. If the predictions are correct, then social insects, which have long served as exemplars of cooperation between individuals, will also be shown to be extraordinary examples of competition within individual genomes.

Background

Organisms are normally very cohesive entities in the sense that their components work together toward their common goal of survival and reproduction. However, there are occasional circumstances where different parts of an organism's genome may be in conflict because they have different possible paths of reproduction [1–3]. Organellar genes transmitted only through eggs may suppress pollen function. Drive elements can spread by killing off gametes lacking them. Transposons that jump to other places in the genome can spread though increased copy number even at some cost to their bearer.

Genomic imprinting provides another likely case of within-genome conflict. An imprinted gene is one with parent-specific gene expression; it is expressed differently according to whether it was inherited from the mother or the father [4]. Often one copy or the other is completely silenced. Differential methylation in the parental germ-lines is thought to underlie imprinting. Whether or not a parent methylates a particular gene in the germ line may affect its expression in the offspring by altering the binding of enhancers or repressors.

Haig's kinship theory of imprinting [5–8] explains how such imprinting may be related to within-genome conflict via kin selection. Kin selection is the process whereby a gene's action affects the transmission of the gene to future generations, not through its effects on offspring, but through effects on other relatives who share the gene [9,10]. The power of this process is proportional to the relatedness between the actor and the individual affected. Kin selection theories have generally assumed that maternally and paternally inherited genes are expressed identically, so that the relevant relatedness coefficients are the average of those pertaining to genes inherited from the mother and father. However, Haig's kinship theory of imprinting explains how separate maternal and paternal coefficients take on meaning for imprinted genes. This has been worked out primarily for sibling competition, where an offspring takes resources from its mother, at some cost to its siblings. In the absence of imprinting, the offspring is selected to weigh its own gain by its relatedness to self (1) and to weigh the cost by its relatedness to the siblings affected (1/2 for full siblings, 1/4 for half siblings). Suppose the cost falls on maternal half siblings (with different fathers) and there is imprinting. The paternally derived gene is not present identical by descent in the half sibling ($r = 0$) so if only this allele is expressed, it will be selected to always be selfish, regardless of the cost to the half siblings. The maternally derived allele has a 50% chance of being present in a half sibling ($r = 1/2$) so if it is the only allele expressed, selfishness will have a net advantage only when the benefit is greater than half the cost to the half sibling. There is therefore potential conflict between the paternally and maternally inherited genes, with the paternal ones favoring selfish behavior under broader conditions than maternal ones.

Of the various evolutionary theories of genomic imprinting, the kin conflict theory sketched above seems to explain the available data most effectively [8,11]. It accounts for why imprinting seems common in mammals and plants, taxa with prolonged provisioning of offspring by their mother. It also accounts for why so many of the known imprinted genes are expressed in embryos or in genetically similar or identical surrogates that act on behalf of the embryo, like placentas or endosperms. Finally, it explains why paternally expressed genes tend to increase the size of the offspring while maternally expressed genes usually tend to decrease it.

The kinship theory of imprinting would be greatly strengthened if it could be tested in other situations in which it makes different predictions. For example, in species where the male provides parental care, one might expect imprinting effects in the opposite direction, with maternally derived genes being more selfish [12]. Queller & Strassmann [13] recently argued that the best novel con-

texts for testing this theory are supplied by the haplodiploid social insects. They also suggested that social insect workers could be so deeply divided by genomic imprinting conflict as to scarcely have any uniquely individual interests. In this paper, I develop the underlying theory and predictions in greater detail.

Social insects are particularly interesting from this perspective for two reasons [13]. First, they have a much wider variety of interactions among relatives than the simple case of transfer of nutrients from parent to offspring; social insects both compete and cooperate with each other in numerous contexts. Second, there are three distinct sources of the kinds of relatedness asymmetries that might make maternally and paternally derived genes conflict (Figure 1). There is multiple mating, as in the standard imprinting case (which works only with half siblings). In social insects, multiple queens can play a similar role. In many social insects, colonies are headed by related queens who are mated to unrelated males. Their offspring are therefore more related through the female side than through the male side. Finally, ants, bees and wasps are Hymenopterans who share the haplodiploid genetic system. Haig [14] first noted that haplodiploidy creates asymmetries between maternal and paternal genes that might favor imprinting. In haplodiploid species, females are diploid and arise from fertilized eggs while males are haploid and arise from unfertilized eggs. As Hamilton (1964) first showed, this leads to an extraordinarily high relatedness of 3/4 among full sisters, providing a possible explanation for why females might work to rear sisters instead of raising their own offspring ($r = 1/2$). The elevated relatedness to full sisters arises because the haploid father contributes exactly the same genes to all his daughters, with no reduction division. Haig therefore argued that paternally expressed genes would be more selected to favor caring for sisters than maternally expressed genes. The condition reverses with sufficient multiple mating by the queen, because then the paternal genes are rarely related. Furthermore, because paternal genes in worker females are absent from their brothers, they should be selected to favor highly female-biased sex ratios [14].

Most work on the kin conflict theory of imprinting has focused on how maternally and paternally derived genes are selected, assuming they have been differentially labelled by the parents. A related but distinct question is the evolution of the labeling itself [12]. When should mothers and fathers put an imprint on their genes? One possibility is that the original imprinting itself has no immediate effects on kin and is selected for unrelated reasons or drifts to fixation. Alternatively, the placing of the imprint by a parent may have an immediate effect on gene expression and social behavior in the offspring and be selected for those effects. For example, if a mother places

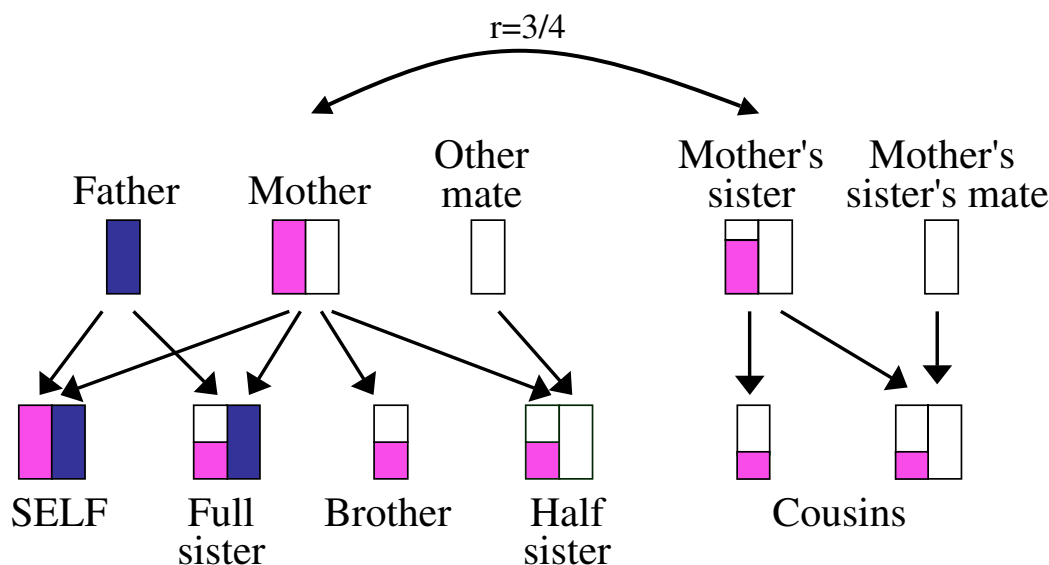


Figure 1
Haplodiploid pedigree. Coloring shows the relationships of the individual labelled "SELF". SELF's matrigenes are colored in pink and patrigenes in blue. Genes unrelated to SELF are all shown in white. Relatives bearing different fractions of pink and blue are those for which there may be conflict between SELF's matrigenes and patrigenes.

methyl groups in a novel location, it might change properties at the binding site of a promoter in her offspring. In this event, one needs to consider the mother's inclusive fitness interests. These are not always the same as the interests of a maternal gene in the offspring because that gene has undergone segregation; it "knows" it is in the offspring whereas a gene in the mother prior to segregation has only a 50% chance of being transmitted to that offspring.

The importance of the distinction between maternal and maternally derived genes renders the terminology potentially confusing. Haig [15] introduced the terms "madumnal" and "padumnal" to describe the genes derived from the mother and father, but these are not very euphonious and have not been adopted, so perhaps it is time for

another try. In their place, I will use the terms "matrigenic" and "patrigenic" (Queller & Strassmann 2002). The "genic" suffix simultaneously evokes both the object of interest (the gene) and the fact that its source (genesis) is what is important. They also have the advantage of having corresponding noun forms: matrigenic and patrigenic. With the addition of these terms, confusion can be avoided by using maternal and paternal to refer only to the genes in the mother and father, or to the strategies of the mother and father. That being said, the problem is somewhat simplified in haplodiploids; because there is no segregation in males, paternal interests are identical to patrigenic interests. The distinction is only important on the female side.

Table 1: Coefficients of relatedness for a haplodiploid female for various female and male relatives

		Full sibling	Half sibling	Own offspring	Offspring of full sister	Offspring of half sister	Mother related by r_{qq} , father unrelated
Females	average	3/4	1/4	1/2	3/8	1/8	$r_{qq}/4$
	patrigenic	1	0	1/2	1/2	0	0
	matrigenic	1/2	1/2	1/2	1/4	1/4	$r_{qq}/2$
Males	average	-	1/2	1	3/4	1/4	$r_{qq}/2$
	patrigenic	-	0	1	1	0	0
	matrigenic	-	1	1	1/2	1/2	r_{qq}

These are regression coefficients that do not include reproductive value differences between males and females. The last column is for relationships like cousins, with mothers related by $r_{qq} = 3/4$ and fathers unrelated.

Derivation of the conflict conditions requires application of kin selection theory. An allele is favored under kin selection if it increases inclusive fitness, which is the sum of all its fitness effects on relatives (Δw_i), including itself, devalued by the coefficient of relatedness of the actor to the individual affected (r_i). In haplodiploids, a complete account of inclusive fitness must also include two kinds of reproductive value variables, as follows:

$$\sum_i \Delta w_i r_i V_i S_i > 0 \tag{1}$$

(see [16,17]). S_i is an adjustment for reproductive value owing to mating success of the two sexes. It takes on values proportional to $1/F$ for females and $1/M$ for males, where F and M are the numbers or fractions of females and males in the population. F and M could be included in diploid equations as well, but are usually omitted because they cancel out at sex-ratio equilibrium of $M = F$. They are included here because of the importance of deviations from sex ratio equilibrium in social haplodiploids. V_i is a distinct sex-specific reproductive value adjustment that applies regardless of sex ratio. It corrects for the fact that diploid females and haploid males contribute differently to distant future generations. Under most conditions, females (as a group) contribute twice as many genes to distant future generation as males, so we will set $V = 1/2$ for haploid males and $V = 1$ for diploid females. Thus, summing separately over males and females gives:

$$\sum_m \Delta w_m r_m / 2M + \sum_f \Delta w_f r_f / F > 0 \tag{2}$$

However, under some conditions, such as when workers produce some of the male eggs, the V 's may take different values [16]. In this paper, I will use equation 2, unless otherwise noted.

Relatedness in haplodiploids has been expressed in two ways [18,19]. The r coefficients used in (1) are regression coefficients, and can be thought of, for any gene in the actors, as the regression of its frequency in beneficiaries on its frequency in itself. Table 1 lists the most important regression r 's used in this paper. Many readers will be more familiar with Hamilton's life-for-life coefficients, which are the regression measures with the standard V adjustments already made (i.e. multiplying the regression measure by 2 for male-to-female relatedness and dividing by 2 for female-to-male relatedness). The reason for keeping the r 's and V 's distinct is to accommodate those cases where the V 's are not in the standard 2 to 1 ratio.

Table 1 lists the standard regression r 's for haplodiploid females, but also adds the separate regression r 's for a female's patrigenes and matrigenes. Only female relatednesses are included, for two reasons. First, males perform few social behaviors in social Hymenoptera. Second, males cannot have conflict between matrigenes and patrigenes because they lack the latter. The separate coefficients are calculated by dividing the frequency (identical by descent) of the gene in question in the relative by its frequency in itself (1/2). The usual regression coefficient is the average of the patrigenic and matrigenic coefficients. Queller & Strassmann [13] used a diagrammatic method where the normal r is instead the *sum* of two maternal and paternal components, which were half of the regression values shown here. In formal theory it seems better to employ the traditional regression-coefficient form, but which method is used makes no practical difference because the factor-of-two difference applies to all r 's, and cancels out in application of Hamilton's rule.

A number of the results derived below concern colonies with a multiply mated queen or with multiple queens. Relatednesses within these colonies are often averages of coefficients in Table 1. For example, if the queen is mated to x males and their sperm is used equally then relatedness among their progeny is:

$$r_{average} = \frac{1}{x}r_{own} + \frac{x-1}{x}r_{other} \quad (3)$$

where r_{own} is relatedness to the individuals in one's own patriline, and r_{other} is relatedness to individuals in the other patrilines. Similarly, when the progeny are equally divided among q queens:

$$r_{average} = \frac{1}{q}r_{own} + \frac{q-1}{q}r_{other} \quad (4)$$

where r_{own} and r_{other} now refer to matriline rather than patrilines. I will not treat the more complex case of societies with multiple, multiply mated queens, because these appear to be very rare, but the principles are the same.

Results

The general procedure adopted below is as follows. First, identify the classes of relatives affected by a behavior and write Hamilton's rule (1) or (2) in a suitable form. Substitute in the relatednesses of the actor to the affected parties. These are generally drawn from Table 1, if necessary averaging using (3) and (4) for multiple mates and multiple queens, respectively. Then solve for the threshold b/c ratio, the ratio above which the behavior is favored and below which it is disfavored. This is carried out separately for unimprinted, matrigenes, and patrigenes, and comparison of the thresholds reveals which is predicted to be selfish (or altruistic) under the widest range of conditions. Also of interest are the corresponding b/c thresholds for when mothers and fathers should imprint. As noted above, the patrigenic threshold in haplodiploids is the same as the paternal threshold. To solve for the maternal threshold, I substitute relatedness of the mother to the parties affected. Each section of the results treats a different category of interaction defined in terms of what parties are affected. The discussion gives more detail on the specific kinds of behaviors that may apply to each category.

Trade-offs between self and female coevals

In the standard imprinting conflict, offspring compete for limited resources, usually supplied by a parent, and have effects on siblings. Consider first how this would work in haplodiploids if the focal female gains at the expense of her sisters [14,20]. More generally, I will then consider not just effects on sisters, but on any female generation-mates which, for lack of a better term, I will call coevals. When there are multiple queens in a colony, coevals among their progeny might include cousins or even non-relatives. Ignoring the first term of expression 2 because it pertains to males, and dividing the second term into one involving effects on a focal female and another involving effects on her female coevals, we have $\Delta w_{f:F} + \Delta w_{coF:F} > 0$ (where

Δw_{coF} is the summed Δw_i for all affected female coevals, or the net cost). If the focal female gains fitness benefits at a fitness cost to coevals, $\Delta w_F = b_F > 0$ and $\Delta w_{coF} = -c_{coF} < 0$, giving benefit/cost threshold of:

$$\frac{b_F}{c_{coF}} > \frac{r_{coF}}{r_F} \quad (5)$$

If the focal female loses direct fitness and her coevals gain, $\Delta w_F = -c_F < 0$ and $\Delta w_{coF} = b_{coF} > 0$, giving cost/benefit threshold of:

$$\frac{c_F}{b_{coF}} > \frac{r_{coF}}{r_F} \quad (6)$$

For the moment, I focus on expression (5) for selfish behaviors. Table 2 shows the threshold b/c ratios for three kinds of genetic structure. Column 1 is for females who come from a single once-mated queen, that is, full sisters. The non-imprinted rule depends on the $r_{coF} = 3/4$ between full sisters and $r_F = 1$ for self. Note first that it differs from the rule for genes expressed in the mother (last row), which derives from the fact that the mother is equally related to the focal female and her coevals. Just as in standard parent-offspring conflict [21,22], females are selected to put more of a cost on their sisters, for any given benefit to self, than their mother is selected to favor.

However, if there is imprinting, the offspring female has divided interests: her matrigenes and patrigenes are selected to disagree because r_{coF} is 1/2 for matrigenes and 1 for patrigenes (Table 2). Matrigenes should be more selfish than patrigenes [14,20,13]. Specifically, matrigenes should favor being selfish and patrigenes should be opposed whenever $1/2 < b_F/c_{coF} < 1$. As in the familiar diploid case, the unimprinted threshold is intermediate between the two imprinted thresholds. However, several important differences emerge. First, imprinting conflict can be important even with single mating. Haplodiploidy by itself creates the necessary asymmetry. Second, in this haplodiploid case, it is the matrigenes that are selected to be selfish and the patrigenes that will be selected to moderate selfishness. The reason is of course that the patrigenes are the same in every full sister, so they value full sisters as much as their own bearers. Third, the patrigenes have an ally in battles against the matrigenes: the mother. This may make it more difficult for matrigenes to win.

Now suppose the single queen has mated multiply, with x males who share reproduction equally (Table 2, second column). r_{coF} must now be averaged using (3). Under multiple mating, non-imprinted genes have a threshold that ranges from 3/4 for one mate to 1/4 for many mates. As expected, as the fraction of full sisters decreases, the region where selfishness is favored increases (threshold b/c ratio

Table 2: Thresholds for favoring female behaviors affecting a trade-off between self and female coevals.

	(1) One queen, singly mated	(2) One queen, x mates	(3) q queens, singly mated
Non-imprinted	$\frac{3}{4}$	$\frac{2+x}{4x}$	$\frac{3+(q-1)r_{qq}}{4q}$
Patrigenic	1	$\frac{1}{x}$	$\frac{1}{q}$
Matrigenic	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1+(q-1)r_{qq}}{2q}$
Patri. > Matri.	always	$x < 2$	$q < 1 + \frac{1}{r_{qq}}$
Maternal	1	1	$\frac{1+(q-1)r_{qq}}{q}$

The numbers represent the benefit/cost ratio above which selfishness is favored (expression 5), and the cost/benefit ratio below which altruism is favored (expression 6). Low values are more selfish. Each column defines one kind of colony structure and each row represents selection on a different kind of gene, the first three in a female offspring and the last in a queen. The "Maternal" conditions are for when a mother would be selected to imprint one of her daughters to perform the action in question. Fathers would be selected to imprint daughters under the patrigenic conditions.

is lower). This change comes entirely from patrigenes. A matrigene is equally related to full sisters and half sisters, so the matrigenic *b/c* threshold remains at 1/2. In contrast, the patrigene threshold drops to 1/*x*, reflecting their zero relatedness to half sisters. This means the direction of imprinting effects should change with mate number. With a single mate, as shown above, the matrigene should act more selfishly than patrigenes. With an effective mate number [23] of 2 or more, matrigenes should be less selfish [13].

Now assume that the competing females come from a polygynous society, where the coeval females in question derive from *q* singly mated, equally reproducing queens, related to each other by *r_{qq}*. The fathers are assumed to be unrelated to each other and to the queens. The relatedness values of the competing females must now be weighted according to (4). The *b/c* thresholds are given in the last column of Table 2. The effect of multiple queens is rather like the effect of multiple males. As queen number

increases, the unimprinted threshold declines from 3/4 to *r_{qq}*/4, so selfishness is easier to evolve. The condition for matrigenes is no longer invariant, but there still appears to be a point at which the direction of imprinting switches: patrigenes will be less selfish than matrigenes (lower *b/c* threshold) when

$$q < 1 + 1/r_{qq} \quad (7)$$

and more selfish when the queen number is larger. This reflects the change from full sisters that are more related through the patrigenes, to cousins that are more related through the matrigenes. Thus, when queens are related by 3/4, matrigenes in their female offspring will be less competitive with at least two queens. If they are related as half sisters (*r_{qq}* = 1/4) queen number must exceed 5. If the queens producing the competing females are unrelated, then matrigenes should never be more competitive than patrigenes. However, in the Discussion section, I note how a linkage between *q* and *r_{qq}* sometimes changes this conclusion.

The maternal condition under multiple queens requires explanation. If we wanted to know how a mother queen would favor transfer between females of the next generation, not knowing which is her offspring, the threshold would still be 1 (i.e. *b > c*). However, we are interested in whether selection would favor a mother placing an imprint that causes her own daughter to do something affecting the daughter and her daughter's female coevals. She cannot imprint the other queen's daughters. For the question of placing an imprint that acts through the daughter, the appropriate *r_F* is the queen's relatedness to her own particular daughter, 1/2 while the appropriate *r_{coF}* is the weighted average of the queen's relatedness to her own daughters and to the daughters of other queens, using (4). This difference will recur in the sections below whenever the queen imprints her daughter in a way that affects that daughter's own fitness, but not when the imprint causes the daughter to only affect other individuals (as in the sex ratio).

The thresholds above apply when females compete only with other females, particularly reproductive competition among adult females such as nest foundresses or queens of multi-queen species. They are not generally appropriate for the context of female larvae soliciting food – the context parallel to the standard imprinting conflict – because that would normally also affect males. The more complicated case with effects on both females and males will be considered below. Because the sex-ratio has important effects in this case, I will treat the sex ratio first.

Sex ratio: trade-offs between males and females

Sex ratio is perhaps the best-studied kind of queen-worker conflict [16,24]. It also affects other questions in haplodiploid social insects, including the origin of sociality. For simplicity, throughout this paper, I will assume that individual males and females are equally costly. When they are not, the formulas can be adjusted by addition of a cost ratio correction, and the results should remain the same except for being expressed in terms of relative investment rather than relative numbers.

In terms of equation 2, we can ask when would it pay to raise one male at the cost of one female, and vice versa. Setting the Δw 's to unity, it is better to produce a male when $r_m/2M > r_f/F$ and better to produce a female when the sign is reversed. The stable equilibrium is when the two sides are equal or

$$\frac{F}{M} = \frac{r_f}{r_m/2} \tag{8}$$

The sex ratio optima for each party are shown in Table 3. Each is the equilibrium F/M that would result if all selection were on one kind of gene. Again, the first column of entries is for colonies with a single singly mated queen. The top and bottom rows in this column summarize the most basic sex ratio theory for haplodiploids [16,24]. Mothers will favor 1:1 sex ratios because $r_m = 1$ and $r_f = 1/2$, meaning they are equally related to their sons and daughters once the reproductive value difference is accounted for (the 2 in equation 8). However, workers in a colony with one singly mated queen will be rearing full sisters ($r_f = 3/4$) and brothers ($r_m = 1/2$), so equation 3 predicts a 3:1 ratio of females to males. As previously noted by Haig [14], the worker's patrigenic and matrigenic alleles will be in conflict if they are expressed differentially. For the matrigenes, $r_m = 1$ and $r_f = 1/2$, so a 1:1 ratio is favored.

For the patrigenes, where $r_m = 0$ and $r_f = 1$, expression (8) predicts an infinite ratio, that is, complete investment in

females. This follows because a worker's patrigene is unrelated to brothers. Under imprinting, then, patrigenes should favor more investment in sisters than matrigenes favor [14]. Thus, the conventional 3:1 equilibrium in the absence of imprinting is not an equilibrium for imprinted genes. At the 3:1 equilibrium there is no selection on workers at the individual level; a brother is just as valuable as a sister. But selection will still operate on imprinted worker genes because 3/4 is above the matrigenic gene equilibrium and below the patrigenic equilibrium. Again, the unimprinted value can be seen as the average of the matrigenic and patrigenic values, provided they are expressed in proportion of females rather than ratios ($3/4 = [0.5 + 1]/2$).

Now consider a queen who has mated multiply with x males who share reproduction equally (Table 3, column 2). Again, $1/x$ of a worker's sisters will be full sisters, and the remainder half sisters (expression 3). Substituting the weighted relatedness in (8) yields a new equilibrium for an unimprinted worker gene: $F/M = (2 + x)/x$. Thus, as is well known, as the number of mates increases, the worker optimum approaches the queen optimum of 1 because workers are symmetrically related to half sister and brothers. The other optima are unchanged from the single mating case. The maternal optimum remains the same as multiple mating does not change her relatedness to offspring, and the same is true for matrigenes in the worker. Curiously, the patrigenic optimum also remains unchanged at 8, even though patrigene relatedness to females decreases (fewer full sisters), because patrigene relatedness to males remains at zero. Here is an instance where the unimprinted optimum is not the average of the patrigenic and matrigenic ones. However, the unimprinted optimum does still provide some measure of the relative importance of matrigenes and patrigenes. As x increases, selection on the patrigenes becomes relatively impotent; any bias patrigenes create towards more sisters gives them a small genetic payoff, as most of those sisters are half sisters who do not share the gene.

Table 3: Sex ratio equilibria

	(1) One queen, singly mated	(2) One queen, x mates	(3) q queens, singly mated
Non-imprinted	3	$\frac{2+x}{x}$	$\frac{3+(q-1)r_{qq}}{1+(q-1)r_{qq}}$
Patrigenic	∞	∞	∞
Matrigenic			
Patri. > Matri.	always	always	always
Maternal			

Each entry is the equilibrium sex ratio F/M, from expression (8), that would result if only the kind of gene specified in column 1 was selected. Columns and rows as in Table 2.

The last column of Table 3 shows the multiple-queen case, with q equally reproductive queens of the same generation, each mated once. Relatedness is now weighted according to (4). The non-imprinted equilibrium is a complicated expression that reduces as expected to 3 when $q = 1$. This same equilibrium of 3 applies for multiple unrelated queens. When queens are related, the investment ratio approaches 1:1 under high queen numbers, an effect similar to multiple mating.

The other optima remain unchanged. Patrigenes in workers are related only to the $1/q$ sibling fraction ($r_f = 1/q$ and $r_m = 0$). The equilibrium F/M remains infinite. For matrigenes the equilibrium F/M remains 1. Thus, as with multiple mating, having multiple queens alters the optimal strategies of non-imprinted genes, but not imprinted genes. Also like multiple mating, the non-imprinted optimum is not the average of the patrigenic and matrigenic ones, but does reflect the degree to which they become less potent through dilution with cousins who are either unrelated (for patrigenes) or less related (for matrigenes).

Queens may also affect sex ratios, but a queen's matrigenes and patrigenes are not differently related to sons and daughters, so there is no reason to expect them to be imprinted under the conflict theory.

Trade-off between female versus coevals of both sexes

When a female stands to gain a fitness benefit, the cost often falls not just on other females (the case considered above) but on the colony output as a whole. For example, if a female reproductive consumes extra resources, there will be less left for other reproductives, both female and male. Consider some party whose relatedness to the focal female is r_F and whose relatedness to that female's coevals is r_{coF} and r_{coM} for females and males respectively. This party performs a behavior that causes the focal female's fitness to change by Δw_F and also causes a fitness change of Δw_{co} to each of n_{coF} coeval females and n_{coM} coeval males. Note that earlier I used Δw to stand for the summed effects on sisters, while here it is more convenient to define Δw as the per sibling fitness change, and then multiply by their number. Using expression 2, with the female term split into separate terms for the coeval females and the focal female, we have

$$n_{coM}\Delta w_{co}r_{coM}/2M + n_{coF}\Delta w_{co}r_{coF}/F + \Delta w_F r_F / F > 0. \quad (9)$$

If the female's behavior is selfish, $b_F = \Delta w_F > 0$ and $c_{co} = -\Delta w_{co} < 0$. This gives a benefit/cost threshold of:

$$\frac{b_F}{c_{co}} > \frac{r_{coF}n_{coF}/F + r_{coM}n_{coM}/2M}{r_F/F} = \frac{1}{r_F} \left(r_{coF}n_{coF} + r_{coM}n_{coM} \frac{F}{2M} \right) \quad (10)$$

If the female's behavior is altruistic, $\Delta w_F = -c_F < 0$ and $\Delta w_{co} = b_{co} > 0$, giving benefit/cost threshold of:

$$\frac{c_F}{b_{co}} < \frac{1}{r_F} \left(r_{coF}n_{coF} + r_{coM}n_{coM} \frac{F}{2M} \right) \quad (11)$$

These results parallel those in (5) and (6), where effects fall on sisters only.

Table 4 shows the threshold b/c (or c/b) ratios for a female acting to affect her own fitness at the expense (or gain) of her coevals. The final row also shows the maternal thresholds for the same fitness transfers. Note first that, if no males are affected ($n_{coM} = 0$) the results of Table 2 are recovered (once n_{coF} is replaced by 1 to account for the change from total fitness to per individual fitness). The conditions in Table 4 depend not only on the female's relatednesses to her full sisters and brothers, but also on the population sex ratio, F/M , because that determines the eventual relative mating success of males and females. Consider first colonies headed by a singly mated queen (first column). The maternal threshold is higher than the non-imprinted offspring threshold; that is, the mother favors less selfishness or more altruism by the daughter than the daughter herself favors. The degree to which this is true depends on n_{coF}/n_{coM} and F/M . The simplest, most natural case to consider is when $n_{coF}/n_{coM} = F/M$, that is, when the action affects male and female coevals in the same proportion as the population sex ratio. When this is true, the maternal threshold is exactly twice the non-imprinted offspring threshold. See Crozier and Pamilo [16] for extended discussion of selection on mothers and non-imprinted offspring genes.

The conditions for matrigenes and patrigenes differ (Table 4, column 1), suggesting that imprinting may be important. However, if the actor affects female and male colony-mates in the same proportion as the population sex ratio, $n_{coF}/n_{coM} = F/M$, then the two conditions both reduce to n_{coF} . Thus, if the effects fall on females and males randomly with respect to their frequencies in the population, no imprinting effects are expected.

However, imprinting strategies are expected to differ if genes are conditionally expressed in situations where the actors consistently harm siblings who differ from the population sex ratio. The matrigenic threshold is lower than the patrigenic one when $F/M < n_{coF}/n_{coM}$. So if the siblings affected are more female biased than the population as a whole, matrigenes are selected to be more selfish than patrigenes. We already noted this for the special case when only females experience the cost. In contrast, the matrigenic b/c threshold is higher when $F/M > n_{coF}/n_{coM}$. So if the siblings affected are more male biased than the population as a whole, matrigenes are selected to be less selfish than patrigenes.

Table 4: Thresholds for favoring female behaviors that affect self and both sexes of coevals.

	(1) One queen, singly mated	(2) One queen, x mates	(3) q queens, singly mated
Non-imprinted	$\frac{3n_{coF}}{4} + \frac{n_{coM}F}{4M}$	$\frac{(2+x)n_{coF}}{4x} + \frac{n_{coM}F}{4M}$	$\frac{(3+(q-1)r_{qq})n_{coF}}{4q} + \left(\frac{1+(q-1)r_{qq}}{4q}\right)\frac{n_{coM}F}{M}$
Patrigenic	n_{coF}	$\frac{n_{coF}}{x}$	$\frac{n_{coF}}{q}$
Matrigenic	$\frac{n_{coF}}{2} + \frac{n_{coM}F}{2M}$	$\frac{n_{coF}}{2} + \frac{n_{coM}F}{2M}$	$\left(\frac{1+(q-1)r_{qq}}{2q}\right)\left(n_{coF} + \frac{n_{coM}F}{M}\right)$
Patri. > Matri.	$\frac{F}{M} < \frac{n_{cof}}{n_{coM}}$	$\frac{F}{M} < \frac{n_{cof}}{n_{coM}} \frac{(2-x)}{x}$	$\frac{F}{M} < \frac{n_{cof}}{n_{coM}} \left[\frac{1-(q-1)r_{qq}}{1+(q-1)r_{qq}}\right]$
Maternal	$n_{coF} + \frac{n_{coM}F}{M}$	$n_{coF} + \frac{n_{coM}F}{M}$	$\left(\frac{1+(q-1)r_{qq}}{q}\right)\left(n_{coF} + \frac{n_{coM}F}{M}\right)$

The numbers represent the benefit/cost ratio above which selfishness is favored (expression 10), and the cost/benefit ratio below which altruism is favored (expression 11). Low values are more selfish. Columns and rows as in Table 2.

Under multiple mating (column 2 of Table 4) the nonimprinted selfishness condition becomes easier to meet (and the altruism condition harder to meet) because of the lowered relatedness to the siblings experiencing the cost. This lowering comes entirely from the patrigenic side of the actor's genome, so the patrigenic side becomes more selfish relative to the matrigenic side. In fact, for $x > 2$, the patrigenic condition is always more selfish than the matrigenic one, no matter what the relationship between n_{bro}/M and n_{sis}/F .

Similarly, with multiple queens (column 3 of Table 4), the non-imprinted b/c condition is easier to meet than with a single queen (column 1) because of the lowered relatedness among siblings with multiple queens. In this case, both matrigenic and patrigenic relatedness is lowered, but the patrigenic more so because patrigenic genes are not at all related to the progeny of other queens. Again, the effect is to accentuate patrigenic selfishness relative to matrigenic selfishness. The condition for when the patrigenic threshold is higher (Table 4, Row 4, Column 3) shows dependence on the population sex ratio as before. However, the right hand side is negative when $q > 1 + 1/r_{qq}$, which means under this condition, the patrigenic threshold is lower (patrigenes should be more selfish), irrespective of sex ratios. Thus, provided queen relatedness is not low, matrigenes should be less selfish than

patrigenes whenever there are more than a few queens. At the limit of zero queen relatedness, the single-queen condition is restored because effects on unrelated individuals are selectively irrelevant.

The same fitness trade-off can be viewed from the viewpoint of a worker. Should she favor a focal female coeval if this has costs on other female and male coevals? For example, should workers allow one of their coevals to become a reproductive when this imposes some cost on the resident queen's reproduction? The same expressions, (10) and (11), can be used, but now the relatednesses are for workers to the parties affected. In this case, the worker's relatedness to the focal female being helped is the same as its relatedness to the coeval females being harmed, $r_F = r_{coF}$, so:

$$\frac{b_F}{c_{co}} > n_{coF} + n_{coM} \frac{r_{coM}F}{r_{coF} 2M} \tag{12}$$

or if the focal female suffers a cost to benefit coevals

$$\frac{c_F}{b_{co}} < n_{coF} + n_{coM} \frac{r_{coM}F}{r_{coF} 2M} \tag{13}$$

The important change is that whereas matrigenes and patrigenes are equally related to self, they are often differently related to coevals.

Table 5 shows the thresholds. These thresholds are generally higher than in Table 4 (i.e. favor the focal female less) because the benefit is going to a female coeval instead of to self (except for the maternal thresholds, which are identical because it is the same fitness tradeoff from the mother's point of view).

Relatednesses to this coeval female are not the same for matrigenes and patrigenes, adding another source of imprinting conflicts. So, under one singly mated queen (Table 5, column 1), where the only imprinting effects in Table 4 were due to sex ratio, there is now consistent imprinting. Now the patrigenic threshold is always lower than the matrigenic. So, for example, patrigenes should more often be selected to favor a sister becoming a queen in the colony, and matrigenes should more often be selected to suppress such an action. The same is true under multiple mating (Table 2, column 2) and multiple queens (column 3).

Trade-off between male versus coevals of both sexes

It is also worth considering actions that aid a focal coeval male at a cost to other coeval males and females. Here we do not consider the viewpoint of the focal male himself, because a haploid male has no paternal genes and cannot have parent specific gene expression. Instead we focus on the worker point of view. Should, for example, a worker

respond to a male's demand for more food if that would impose a cost on other male and female brood? From (2), we obtain an expression parallel to (9)

$$n_{coM}\Delta w_{co}r_{coM}/2M + n_{coF}\Delta w_{co}r_{coF}/F + \Delta w_M r_M/2M > 0 \quad (14)$$

differing only in the final term applying to a male instead of a female. The worker's relatedness to the focal male being helped is the same as her relatedness to other coeval males being harmed, $r_M = r_{coM}$, so:

$$\frac{b_M}{c_{co}} > n_{coM} + n_{coF} \frac{r_{coF} 2M}{r_{coM} F} \quad (15)$$

or if the focal male suffers a cost to benefit coevals

$$\frac{c_M}{b_{co}} > n_{coM} + n_{coF} \frac{r_{coF} 2M}{r_{coM} F} \quad (16)$$

Table 6 shows the thresholds. The key feature with respect to imprinting is that worker patrigenes are unrelated to the males produced by the queens ($r_{coM} = 0$). Therefore worker patrigenes would always favor suppression of brothers. This result, coupled with the previous one in which matrigenes tend to suppress sisters, is closely related to the sex ratio result derived earlier. But it shows that similar logic applies not just for pure fitness transfers between the sexes, but also when an individual of one sex is favored at a cost to both sexes of its siblings.

Table 5: Thresholds for worker behaviors that affect trade-offs between one of their female coevals versus both male and female coevals.

	(1) One queen, singly mated	(2) One queen, x mates	(3) q queens, singly mated
Non-imprinted	$n_{coF} + \frac{n_{coM}F}{3M}$	$n_{coF} + \frac{xn_{coM}F}{(2+x)M}$	$n_{coF} + \frac{(1+(q-1)r_{qq})}{(3+(q-1)r_{qq})} \frac{n_{coM}F}{M}$
Patrigenic	n_{coF}	n_{coF}	n_{coF}
Matrigenic	$n_{coF} + \frac{n_{coM}F}{M}$	$n_{coF} + \frac{n_{coM}F}{M}$	$n_{coF} + \frac{n_{coM}F}{M}$
Patri. > Matri.	never	never	never
Maternal	$n_{coF} + \frac{n_{coM}F}{M}$	$n_{coF} + \frac{n_{coM}F}{M}$	$n_{coF} + \frac{n_{coM}F}{M}$

The numbers represent the benefit/cost ratio above which favoring the one female coeval is selected (expression 12), or the cost/benefit ratio below which disfavoring her is selected (expression 13). Low values favor the focal female and high value favor the male and female coevals. Columns and rows as in Table 2.

Table 6: Thresholds for worker behaviors that affect trade-offs between one of their male coevals versus both male and female coevals.

	(1) One queen, singly mated	(2) One queen, x mates	(3) q queens, singly mated
Non-imprinted	$n_{coM} + 3n_{coF} \frac{M}{F}$	$n_{coM} + (2x-1)n_{coF} \frac{M}{F}$	$n_{coM} + \frac{(2+q)n_{coF}M}{qF}$
Patrigenic	∞	∞	∞
Matrigenic	$n_{coM} + n_{coF} \frac{M}{F}$	$n_{coM} + n_{coF} \frac{M}{F}$	$n_{coM} + qn_{coF} \frac{M}{F}$
Patri. > Matri.	$n_{coF} \neq 0$	$n_{coF} \neq 0$	$n_{coF} \neq 0$
Maternal	$n_{coM} + n_{coF} \frac{M}{F}$	$n_{coM} + n_{coF} \frac{M}{F}$	$n_{coM} + n_{coF} \frac{M}{F}$

The numbers represent the benefit/cost ratio above which favoring the one male coeval is selected (expression 15), or the cost/benefit ratio below which disfavoring him is selected (expression 16). Low values favor the focal male and high values favor the male and female coevals. Columns and rows as in Table 2.

Table 7: Thresholds for a worker replacing one of the queen's male eggs with her own male egg.

	(1) One queen, singly mated	(2) One queen, x mates	(3) q queens, singly mated
Non-imprinted	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{q} \times \frac{1}{2} + \left(\frac{q-1}{q}\right) \frac{r_{qq}}{2}$
Patrigenic	0	0	0
Matrigenic	1	1	$\frac{1}{q} \times 1 + \left(\frac{q-1}{q}\right) r_{qq}$
Patri. > Matri.	never	never	never
Maternal	2	2	$\frac{2}{q} + \left(\frac{q-1}{q}\right) 2r_{qq}$

The numbers represent the benefit/cost ratio above which replacement is favored (expression 17), so low values favor replacement. Columns and rows as in Table 2.

Trade-offs between males of maternal versus daughter generations

One reproductive option that remains open to many workers in haplodiploids is the laying of male eggs, which does not require workers to be inseminated [18,24]. Here I will assume the simplest case where the workers have the option of replacing a queen-laid male. Worker laying of male eggs changes the sex-specific reproductive values, so that females are no longer exactly twice as valuable as males. Therefore we use the more general expression (1) instead of expression (2). Let b_{wM} be the benefit to the workers son and c_{qM} be the cost the queen's son, while r_{wM} and r_{qM} are the corresponding relatednesses to these

males. Replacing a queen's male with a worker male is favored when

$$\frac{b_{wM}r_{wM}}{V_M} > \frac{c_{qM}r_{qM}}{V_M} \text{ or } \frac{b_{wM}}{c_{qM}} > \frac{r_{qM}}{r_{wM}} \tag{17}$$

The reproductive value of males depends on the fraction of males that are produced in the population [16,25], but here it cancels out because there are no females affected. If workers sometimes mistakenly replace a queen's female egg, or if there are other costs to the colony resulting in reduced female production, then terms for effects on females would need to be included, and reproductive values would need to be retained.

Table 8: Thresholds for a worker preventing another worker from replacing a queen's son with her own son (worker policing).

	(1) One queen, singly mated	(2) One queen, x mates	(3) q queens, singly mated
Non-imprinted	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{q} \times \frac{1}{2} + \left(\frac{q-1}{q}\right) \frac{r_{qq}}{2}$
Patrigenic	0	0	0
Matrigenic	1	1	$\frac{1}{q} \times 1 + \left(\frac{q-1}{q}\right) r_{qq}$
Patri. > Matri.	never	never	never
Maternal	2	2	$\frac{2}{q} + \left(\frac{q-1}{q}\right) 2r_{qq}$

The numbers represent the benefit/cost ratio above which replacement is favored (expression 18), so low values favor replacement. Columns and rows as in Table 2.

Table 7 shows the thresholds. With a single once-mated queen, the condition for non-imprinted worker genes to replace a queen-laid male is $b/c > 1/2$. As is well known, a female is more related to her own son ($r = 1$) than to the queen's son ($r = 1/2$), so she will replace it unless the b/c ratio is low. Similarly, the queen is twice as related to her son as to her worker's son, so her b/c threshold for allowing the worker to replace her egg is 2. If the behavior simply substitutes one freshly laid male egg by another, then b may be about the same as c . The non-imprinted condition is the average of $b/c > 1$ for matrigenes and $b/c > 0$ for patrigenes. Thus, laying of male eggs by workers will be selected more on patrigenes, reflecting the fact that a worker's patrigene is never present identical by descent in her brothers, who have no father.

Multiple mating does not change these conditions. The mates, single or multiple, do not contribute to the males being replaced. With multiple queens, relatedness is diluted by the presence of the additional queens, but the relative positions of the four parties remain the same. With respect to imprinting, it remains true that patrigenes should be selected to replace the queen's males, while matrigenes should do so only under stricter benefit/cost conditions.

If workers do try to lay male eggs, other workers have the choice of either accepting it or trying to prevent it [26]. The latter is called worker policing, and it could take the form of workers destroying each other's eggs, or of workers preventing each other from becoming reproductively active. Policing is favored when:

$$\frac{c_{wM}}{b_{qM}} < \frac{r_{qM}}{r_{wM}}. \tag{18}$$

This is the same threshold as (17) but with two changes. First, the queen's sons get the benefit instead of the cost. Second, we now take the perspective not of the laying worker, but of another worker, so the relevant relatednesses are for a non-laying worker to a laying worker's sons and to the queen's sons. Table 8 shows the thresholds. Maternal thresholds are generally unchanged from Table 7, because from the queen's point of view, this is the same trade-off between a queen son and a worker son. The exception is the multiple-queen case because, as noted previously, the mother can put an imprint only on her daughters. Worker thresholds are different because now we are considering a non-laying worker's viewpoint. With one singly mated queen (column 1) non-imprinted genes will not generally favor policing because workers are less related to the queen's son ($r_{qM} = 1/2$) than to another worker's son ($r_{wM} = 3/4$). But patrigenes and matrigenes differ. Patrigenes are completely unrelated to the queen's sons and therefore do not favor policing of other workers. Matrigenes are twice as related to the queen's sons ($r_{qM} = 1$) than to other worker's sons ($r_{wM} = 1/2$) and will therefore tend to favor policing.

Multiple mating (Table 8, column 2) tends to promote policing in non-imprinted genes because workers become less related to each other. The well-known unimprinted prediction is that if $b = c$, workers should police each other only if the number of mates exceeds 2 [26]. However, the imprinted conditions are independent of mate number. The matrigenes are always twice as related to the queen males as to worker males and so they would be selected to

favor policing. The patrigenic relatedness to worker sons changes with mate number, but its relatedness to the queen's sons is always zero. Patrigenes are therefore always selected not to police (favoring other worker's males over the queen's) but the strength of this selection is expected to weaken with mate number because the patrigene will also be unrelated to many of the worker males benefited.

Similar results hold for multiple queens (Table 8, column 3). Again, the non-imprinted condition switches from not favoring policing at low queen numbers (when $q = 1$, c/b must be less than $2/3$) to favoring policing at high queen numbers (c/b must be less than 2). The patrigene remains opposed to policing at all c/b levels. The matrigene condition has become dependent on queen number, but the c/b threshold is always greater than 1, so that matrigenes still generally favor policing.

Kin recognition

Distinguishing colony-mates from non-relatives will normally be favored by both matrigenes and patrigenes. Imprinting might be expected to be involved in colony recognition only when neighboring colonies tend to be related through one parent but not the other. For example, if adjacent colonies were produce by budding, and the queens of these colonies mate with males who have dispersed, patrigenes in the queens' female progeny would be more favored to recognize and exclude members of neighboring colonies.

Females could gain inclusive fitness by favoring their closest relatives within their colony, for example favoring full sisters over half sisters, though there is little evidence that they do (Keller 1997). Reeve [27] suggested that imprinting and the accompanying disagreement between matrigenes and patrigenes might be relevant to this absence of within-colony discrimination. From expression (2), genes affecting a closer colonymate and more distant colonymate are expected to be selected according to:

$$\frac{c_{distant}}{b_{close}} < \frac{r_{close}}{r_{distant}} \tag{19}$$

Table 9 shows the relevant thresholds for two kinds of within-colony discrimination. Column 1 is for favoring a female of one's own patriline over a female of another patriline. In words, patrigenes value full sisters very highly, while matrigenes have no relatedness stake in favoring full sisters, favoring them only if the benefit exceeds the cost to half sisters. Hence the failure to see such discrimination could result from matrigenic resistance [27]. The same explanation is not so strong for discrimination of matriline in multiple-queen colonies

(Table 9, column 2). In this case, the thresholds apply both to discrimination of females and discrimination of males (by females). Again, patrigenes are more strongly selected to discriminate (unless $r_{qq} = 0$). However, matrigenes are also more related to their own matriline than to other matriline, so c/b ratios may often be in a region where matrigenes would favor discrimination. In this range, there would be no conflict between patrigenes and matrigenes.

Table 9: Thresholds for favoring ones own matriline or patriline over another in the same colony.

	(1) One queen, n mates; favor females of own patriline	(2) q queens singly mated; favor own matriline
Non-imprinted	3	$\frac{3}{r_{qq}}$
Patrigenic	∞	∞
Matrigenic	1	$\frac{1}{r_{qq}}$
Patri. > Matri.	always	always
Maternal	1	$\frac{1}{r_{qq}}$

The numbers represent the benefit/cost ratio above which discrimination is favored (expression 19). Low values favor more discrimination. Columns and rows as in Table 2.

Discussion

Haig [14] first proposed that haplodiploidy would make social insects prone to imprinting effects for both sex ratio and for helping behavior. Queller & Strassmann [13] suggested that imprinting effects would be more pervasive, covering most areas of social conflict. The inclusive fitness expressions in the present paper provide a more rigorous foundation for this claim. Numerous predictions follow about imprinting effects in social insects, many of which are summarized in Table 10. While mechanistic studies are required to tell us how imprinting works, Haig's kin conflict theory provides us with a plausible "why". In addition, it offers promising predictions as to who, what, where, and which direction. What behavioral contexts are expected to lead to kin conflict between matrigenes and patrigenes. Who are the expected players? Where do we expect to see the conflict expressed; what tissues will show parent-specific gene expression? Which way will matrigenes and patrigenes push in each context?

Table 10: Predictions about imprinting effects in haplodiploid social insects.

Behavior	Expressed in	Under condition(s)	Action of patrigenes	Action of matrigenes
Suppressing excess demands by female larvae (Table 5)	Workers	Any queen or mate number	Less suppressive	More suppressive
Suppressing excess demands by male larvae (Table 6)	Workers	Any queen or mate number	More suppressive	Less suppressive
Competition among coeval queens or foundresses (Table 2)	Reproductive females	One queen, singly mated	Less competitive	More competitive
		One queen, mated more than twice	More competitive	Less competitive
		Multiple related queens, singly mated	Usually less competitive	Usually more competitive
		Multiple unrelated queens, singly mated	No imprinting	No imprinting
Sex ratio: e.g. killing male larvae, harassing male adults (Table 3)	Workers	Any queen or mate number	Favor females	Favor males
	Queens	Any queen or mate number	No imprinting	No imprinting
Helping queen(s) or leaving to reproduce (Table 4)	Females	One queen, singly mated, benefits not sex-biased	No imprinting	No imprinting
		One queen, singly mated, benefits female biased	More altruistic	More selfish
		One queen, singly mated, benefits male biased	More selfish	More altruistic
		One queen, singly mated, split sex ratios	More altruistic in female-biased; more selfish in male-biased	More selfish in female-biased; more altruistic in male-biased
		One queen, more than 2 mates	More selfish	More altruistic
	Multiple queens, benefits not sex-biased	More selfish	More altruistic	
	Workers (Table 5)	All	Aid selfishness	Force helping
Adding a daughter queen, or replacing old queen with daughter queen (Table 2 or 4)	Daughter queen to be added	One queen, singly mated	No imprinting or less in favor	No imprinting or more in favor
		One queen, more than 2 mates Many related queens	More in favor Depends on specific conditions	Less in favor Depends on specific conditions
	Old queen Workers (Table 5)	Any queen or mate number Any queen or mate number	No imprinting Favors daughter queens more	No imprinting Favors old queens more
Become a worker or a queen (Table 2 or 4)	Female affected	One queen, singly mated	No imprinting or worker	No imprinting or queen
		One queen, more than 2 mates Many related queens, new queens from single generation of old queens	Queen Usually queen	Worker Usually worker
	Old queen Workers (Table 5)	Any queen or mate number Any queen or mate number	No imprinting Favors queen more	No imprinting Favors worker more
Division of colony between mother queen and daughter (Table 4)	Daughter queen	One queen, singly mated No sex ratio bias	Unimprinted	Unimprinted
	Daughter queen Mother queen Workers (Table 5)	One queen, multiply mated Any mate number Any mate number	Favor self more Unimprinted Favor daughter queen more	Favor mother queen more Unimprinted Favor old queen more
Excess food demands (Table 4)	Female larvae	One queen, singly mated, no sex bias	No imprinting	No imprinting
		One queen, more than 2 mates	More demanding	Less demanding

Table 10: Predictions about imprinting effects in haplodiploid social insects. (Continued)

		Many queens	Depends on queen number & relatedness	Depends on queen number & relatedness
Laying of eggs in queenless colonies	Workers	One queen, singly mated	Lay fewer eggs, help more	Lay more eggs, help less
		One queen, mated more than twice	Lay more eggs, help less	Lay fewer eggs, help more
		Multiple related queens, singly mated	Lay more eggs, help less	Lay fewer eggs Help more,
Replacement of queen's male eggs by worker's male egg (Table 7)	Replacing worker	Any queen or mate number	Lay male eggs	Lay fewer eggs
Policing of worker male eggs in queenright colonies (Table 8)	Other workers	Any queen or mate number	Less prone to police	More prone to police
Queen killing to allow worker male production (Table 8)	Workers other than the egg layer	Any queen or mate number	More prone to kill queen?	Less prone to kill queen?
Colonymate discrimination	Workers	Neighboring colonies have related queen, unrelated queen mates	Discriminate more	Discriminate less
		Most other structures	No imprinting	No imprinting
Patriline discrimination	Workers	One queen, multiply mated	Discriminate more	Discriminate less
Matriline discrimination	Workers	Multiple singly-mated related queens	Discriminate more	Discriminate less

When costs and benefits are said to be female biased, it means more female biased than the population sex ratio ($f/m > F/M$). Males are assumed to be queen produced unless otherwise noted.

Predictions: interactions among queens or foundresses

Some of the simplest and most interesting predictions concern issues of trade-offs among female coevals (Table 2). Among females who are full sisters (daughters of one singly mated queen), patrigenes should be more altruistic and matrigenes more selfish, a result due entirely to the relatedness asymmetries engendered by haplodiploidy [13,14,20]. However, sufficient multiple mating should reverse this condition; matrigenes should be more altruistic and patrigenes more selfish.

This context provides an excellent opportunity for comparative tests, with the best context being competition among foundresses or queens [13]. Competition among *Polistes* wasp foundresses in those species where they are often full sisters [28–30], should be driven primarily by matrigenes. The lethal fighting among honey bee daughter queens, who come from a multiply mated mother [31,32], should be driven more by patrigenes. Finally, competition among unrelated foundresses, as in most ants [33], should not show imprinting effects.

Examples that fit the category of multiple queens (Table 2, column 3) are rarer. Polygynous societies are common [34]. However, in many cases the queens of these societies

were not themselves produced by many queens. Instead, they are highly related because new queens are produced only on occasions when colonies that have reduced to a one or a few queens [35,36]. This means cohorts of competing queens derive from the genetic structure closer to column 1 of Table 2. Column 3 pertains to competing queens who are themselves the progeny of multiple queens. Some of the highly polygynous ants may qualify [37–39]

The predictions for these polygynous species are less straightforward than for monogynous ones. Patrigenes are predicted to be less selfish when $q < 1 + 1/r_{qq}$ (expression 7). This makes it appear that patrigenes are less selfish only when queen numbers are quite low, but this neglects an important linkage that may occur between q and r_{qq} [36]. When cohorts of new queens are produced by an older generation of old queens,

$$r_{qq} = \frac{3}{4q} + \frac{(q-1)r'_{qq}}{4q}, \tag{20}$$

where r'_{qq} is relatedness of the old queens. That is, $1/q$ of the new queens are full sisters related by $3/4$ and the

remainder are related only through their mothers ($r_{qq}'/4$). At equilibrium $r_{qq} = r_{qq}'$, or

$$r_{qq} = \frac{3}{1 + 3q}. \quad (21)$$

Substituting this into the condition for patrigenes being less selfish than matrigenes (expression 7) yields $q < 1 + (1 + 3q)/3$, which is always true. Thus this linkage between queen number and relatedness causes expression (7) to normally be satisfied, so patrigenes should generally be less selfish, that is, less prone to favor becoming a queen (at least for this requeening scenario; others need more study).

All the thresholds just discussed in the context of selfish behavior also apply for altruism of one foundress towards another. Wherever "less competitive" appears in Table 10, "more altruistic" can be substituted, and wherever "more competitive" appears, "less altruistic" can be substituted. Thus, patrigenes should be more altruistic when the foundresses were produced by a singly-mated queen, and matrigenes when they were produced by a multiply mated queen.

Predictions: sex ratio

Predicted imprinting effects on worker genes affecting sex ratio are simple (Table 3). Regardless of colony structure, patrigenes should tend to have effects in the direction of rearing more females, and matrigenes in the direction of rearing more males. Thus worker killing of male larvae as a means of control of sex investment [40] should be coded by patrigenes as should preferential feeding of female larvae. Sometimes behaviors towards adults may also be affected. If the worker harassment of adult males observed in some species [41] is a means of reducing investment in males, then this behavior should also be most favored by patrigenes.

Predictions: helping versus leaving and reproducing

Haig (1992) suggested that the high relatedness of patrigenes in singly mated single-queen colonies should mean that patrigenes would be selected to favor helping more than matrigenes will. This would be true for the case he considered where workers rear only sisters (Table 2) but we need to consider that they normally also raise brothers, to whom opposite asymmetries apply. In fact, in colonies with one singly mated queen, when both sexes are raised in proportion to the population sex ratio, the asymmetries cancel out, and there is no difference in average patrigene and matrigene relatedness to siblings (Table 4, column 1). We therefore predict no imprinting effects.

In some ways this conclusion mirrors the history of ideas about non-imprinted helping. Hamilton [9] proposed

that helping was easier to evolve in the haplodiploid Hymenoptera because of the high 3/4 relatedness to sisters, an argument that neglected brothers, to whom workers are 1/4 related (including the halving due to relative reproductive value). If sisters and brothers are helped in proportion to the population sex ratio, there is no net advantage to haplodiploidy. A net advantage applies only if the helpers aid is female-biased (compared to the population) and a net disadvantage applies if the aid is more male-biased [16].

Similarly, if the help given to siblings is predictably biased towards one sex, relative to the population ratio, imprinting effects can be favored. If help is biased towards sisters, patrigenes favor it more than matrigenes, because patrigenes are always present in sisters. If help is biased towards brothers, matrigenes favor it more than patrigenes. Many hymenopteran social insects have split sex ratios, where some colonies are strongly female biased, and others strongly male-biased [42]. In singly mated single-queen species with split sex ratios, patrigenes should tend to favor helping more in the female-biased colonies and matrigenes should tend to favor it more in the male-biased colonies.

Biases towards one sex or the other can also result from timing. In annual social insects like *Polistes* wasps or *Bombus* bees, workers are first reared by the queen, and then the workers rear reproductives. If colonies are protogynous, rearing reproductive sisters before brothers, then a time is reached at which females could decide not to work, but instead become reproductives for the next year, with the costs falling entirely on the late-season brothers. Staying and helping brothers should be more matrigenic, and leaving more patrigenic. The opposite result is predicted in protandrous societies where females make a decision on whether to leave versus staying to help late sisters. This logic is most likely to apply to taxa lacking strong morphological castes, like *Polistes* or *Bombus*, but it might apply in species with castes when females have some control over their own caste fate.

Sex ratio effects on imprinting remain when the queen is multiply mated, but they tend to be dominated by an additional kind of asymmetry that does not cancel out (half sisters share matrigenes, but not patrigenes). When there are more than two mates, matrigenes should favor helping more than patrigenes, regardless of sex ratio (Table 4, column 2, row 4). A similar conclusion can be drawn for multiple queens (Table 4, column 3, row 4).

In species where colonies vary in the number of mates or queens, one can predict that helping will be driven more by patrigenes in the colonies with one singly mated queen, and by matrigenes in the more complex colonies.

This result is driven in part by the pure relatedness asymmetries that apply even in the single once-mated queen case, but it is reinforced by the sexual specialization of colonies of different types. Singly-mated single queen colonies should tend to specialize in rearing females because workers gain the 3/4 relatedness advantage, leaving male production to colonies with multiple mates, or multiple queens [43]. As noted above these biases lead to opposite imprinting effects.

The examples mentioned above have focused on species without morphological castes, in which the decision to help or leave is a behavioral decision made by adults. In other species the same decision is made earlier, when physiological switches determine who develops as a morphological worker or queen. So, for example, a female ant larva at the point of making this decision would be predicted to be imprinted as described above.

In many cases, however, caste is controlled by feeding, so workers may exert control over whether their coeval females help or reproduce. Worker matrigenes should tend to be more in favor allowing coeval females to develop as reproductives, while patrigenes should be more in favor of coercing coevals into working (Table 5).

Predictions: adding daughter queens to the colony

In some species, daughters may try to become queens in their natal colony [17]. This is expected to reduce reproduction of other queens because of limited resources. To the extent that these costs fall purely on reproduction of the queen(s) of the old generation, the thresholds should be the same as in the last section (Table 4). However, to the extent that the costs fall on coevals making the same decision, this amounts to competition among female coevals (Table 2). Often both considerations will need to be included.

Consider first a singly mated single-queen species. An individual may try to insert herself as an additional queen, or may try to replace the old queen. Here, if costs fall on the reproduction of the old queen, no imprinting is expected in the absence of sex ratio effects (Table 4, column 1). However, there may be consistent sex ratio effects. Recruitment of new queens may occur at different or partially different times than male production, and these times are almost by definition times of biased investment towards females. This suggests that matrigenes will be more selected to reproduce and patrigenes more selected to help.

Even if this sex ratio effect did not apply, a related consideration leads to the same conclusion. A daughter who becomes a new queen may not just be decreasing the old queen's reproduction; she is also taking a place of her sis-

ter aspirants to queenship. That is, by becoming a reproductive she takes reproduction away from a sister who would otherwise have occupied the same place, or she reduces the share of the colony reproduction of coevals who also become queens. In interactions among full sisters, matrigenes will be more competitive (more in favor of staying as a queen), and patrigenes more altruistic (more in favor of helping or of being a queen elsewhere; Table 2, column 1).

In species that reproduce only by colony fission, reproductives have no option of leaving to nest alone. Daughter queens must always add to the parental colony, or else do the equivalent by taking part of the parental colony in a fissioning event. Here again the decision may be made at the stage of morphological caste determination. For example, in stingless bees of the genus *Melipona*, up to 20% of developing females become queens, even though only a very few will inherit the colony or a daughter colony. Though a large waste to the colony, to each excess queen, the chance of outcompeting her sisters to becoming a high-payoff reproductive is worth the cost [44]. As *Melipona* is singly mated [45], matrigenes are predicted to favor this competitive development as queens more than patrigenes (Table 2, column 1).

In multiply mated species ($x > 2$), the condition reverses. Whether costs fall on the old generation of queens (Table 4, column 2) or on coevals (Table 5, column 2) patrigenes are predicted to be more selfish.

Multiple-queen species are more difficult to predict without further specification. If the costs fall on coevals of both sexes, then patrigenes should be more selfish (Table 4, column 3). However, exceptions could occur if the effects are female biased ($n_{coF}/n_{coM} > F/M$) and, as noted above, investment is likely to be female biased at this time. At the extreme, where all costs fall on female coevals, then patrigenes should be less selfish under condition (7). Recall that this condition, though it appears to be met only for low queen number, is actually always satisfied when expressions (20) and (21) describe the relationship between queen number and queen relatedness. Because the predictions depend so much on the particulars, no prediction is listed in Table 10 for the multiple queen case.

Workers may exert some control over whether a daughter queen (their coeval) is added. Worker patrigenes should be more in favor of adding a new queen and worker matrigenes more likely to suppress new queens (Table 5). The only exception is if none of the costs fall on coeval males ($n_{coM} = 0$). If the cost falls only on female coevals, then there would be no predicted imprinting effects because in

workers both matrigenes and patrigenes are as likely to be in one female coeval as another.

Predictions: colony division

Some social insects, such as honey bees, stingless bees, and army ants, reproduce by colony fission. Part of the original colony's resources, including workers, are allocated to daughter queens, while the old queen retains the rest. Though this division might be influenced by queen signals, it is presumably most directly controlled by workers, who decide where to go and what to bring with them [45,46]. The workers face a choice between the original queen and one of their female coevals, so the predictions are similar to those involved in the acceptance of a daughter queen (Table 5). Patrigenes should be more in favor of supporting the daughter queen than matrigenes, basically because the patrigene is unrelated to any brothers that would be produced by the queen. Therefore imprinted genes causing workers to side with the daughter should be expressed from the patrigene only and those causing workers to stay with the old queen should be expressed from the matrigene only.

The daughter queen herself might influence the division of the colony, perhaps by signalling. Under single mating, these effects should be unimprinted in the absence of sex ratio biases (Table 4). With multiple mates, as in honeybees, patrigenes should be more selected than matrigenes to attract investment from workers (Table 4). The old queen's efforts to attract investment should not be imprinted because her matrigenes and patrigenes are equally related to all offspring.

Predictions: demands for excess care and response

Most thinking on imprinting in mammals and plants conflict has focused on the demands by offspring for additional food [8,11]. In the standard diploid case, offspring demands are imprinted while the parental response should not be. Social haplodiploids should show almost the reverse pattern; the demanding offspring should not necessarily be imprinted, but the responding care-givers, the workers, should be.

Male demands cannot show differential expression between matrigenes and patrigenes because they possess only the former. Demands of female reproductives could be imprinted, but in the simplest case, they are not expected to be. Because this is a trade-off between a female and her coevals of both sexes, it is similar to the case of helping versus leaving to reproduce (Table 4). With one singly mated queen, and no sex bias, the relatedness asymmetries cancel out so that matrigenes and patrigenes are equivalently related to their coevals (Table 4, column 1). Sex biased costs could cause imprinting in ways parallel to those noted in the "helping" section. Under multiple

mating (column 2) patrigenes should become more selfish than matrigenes. A similar effect occurs under multiple queens (column 3) unless, as noted above, the linkage between r_{qq} and q (expressions 19 and 20) changes this conclusion.

The response by workers is closely related to the worker sex ratio results, in which patrigenes favor females and matrigenes favor males. If a female tries to obtain too much food at the expense of her coevals, worker suppression is likely to be coded by patrigenes (Table 5). If a male tries to obtain too much, it is worker patrigenes that should suppress it (Table 6).

Predictions: worker laying of male eggs and policing

In many species, workers will lay male eggs when the colony has lost its queen [47,48]. A worker must then decide whether to lay male eggs or to help rear male eggs laid by others. If the colonies do not requeen or otherwise produce new daughters, this laying of male eggs amounts to pure competition among female coevals, with thresholds in Table 2. In singly mated single-queen colonies, matrigenes should be more selected to lay eggs than patrigenes. The reverse is predicted for multiply mated single-queen colonies like honeybees. In multiple-queen colonies this context seems less likely to occur, as they typically can requeen.

Even when the queen is present, workers in some species may replace the old queen's sons [47,48], a class to which the worker patrigenes are unrelated. Patrigenes should therefore be selected to favor this behavior more than matrigenes (Table 7). Thus, there is an interesting comparative prediction in singly mated single-queen colonies, where matrigenes favor worker laying more in queenless colonies, and patrigenes more in queenright ones.

Other workers may police this worker laying, acting in favor of the queen's sons [26]. Such policing of worker laying by other workers in queenright colonies will be more favored by matrigenes than patrigenes, because the patrigenes are unrelated to the queen's sons (Table 8).

These predictions are based on the most straightforward case, in which a laying worker can always identify a queen-laid male for replacement. In reality, the situation may be more complicated. First, if a worker cannot distinguish sex of brood, her replacement of the queen's egg would reduce the queen's female reproduction as well as her male reproduction. This is true even if the replaced egg would have produced a sterile worker, because a decrease in colony output that follows reduction in worker number would normally reduce the number of reproductive females as well as males. Even a worker who

successfully replaces only the queen's sons may have some negative effects on the queen's daughters through the reduction in colony output due to her pursuing of reproduction instead of work. When effects on females are significant, new predictions will need to be generated. The equations will need to incorporate the level of worker laying and its effect on the reproductive value (V_i) which conveniently cancel out when we consider effects on males alone.

Predictions: kin recognition

Colony-mate recognition and discrimination would not be expected to be imprinted, unless neighboring colonies are related through fission. Then neighboring colonies would tend to share matrigenes, but if queens are outbred, there would be no patrigenes sharing. In such species patrigenes should favor colony-mate discrimination more than matrigenes.

If workers are able to discriminate within their own colony, patrigenes should be driving this more than matrigenes (Table 9). It is obvious why this should be so for discrimination of patriline. But it is also true for discrimination of matriline in colonies with related singly mated queen. This is because matriline is actually better defined by their patrigenes because all members share it. Members of a matriline may share different matrigenes, because the mother has two genes to contribute, and these two are partially shared with other matriline through queen relatedness.

Predictions: where should imprinting effects be expressed?

One of the pieces of evidence supporting Haig's kin conflict theory of imprinting is that so many examples of parent specific gene expression come from embryos, placentas and endosperms, exactly where they are expected if the conflict is over how much the embryo gets relative to its siblings. Social insects provide many new contexts for imprinted effects.

Just as the placenta carries out the function of promoting embryo growth, we can ask what tissues are expected to carry out the functions described in the preceding sections. My own ignorance of the details of insect physiology prevents me from being too specific, but some general points can be made.

Many of the relevant actions are behavioral in nature. For example, should workers kill males? Should they lay eggs or remove the eggs of others? Should they acquiesce to larval demands for more food? Should they go with the old or new queen? It should be expected then that genes expressed in brains and other nervous tissues will sometimes show parent-specific gene expression.

Behavioral actions usually require information, so one might expect sensory organs to also be involved. Chemoreceptors are especially good candidates, both because chemoreception is widely used and because some receptors may be specific to the relevant contexts. For example, receptors of the pheromone that marks queen but not worker eggs in honeybees, and therefore allows worker policing [49], may be imprinted. A more general-purpose modality like vision may be harder to modify for these specific purposes without harming its general functioning. At the other end, providers of information, such as exocrine glands, might also be involved.

All of the conflicts are basically reproductive in nature, but some would directly involve the reproductive organs. Should a queen try to outreproduce the other queens in the colony? Should a worker develop her ovaries to try to lay eggs? Therefore we may expect to see imprinting effects in ovarian tissues, or in the endocrine glands responsible for their development.

Other conflict contexts may involve direct physical confrontation, such as between *Polistes* cofoundresses or daughter honey bee queens. Imprinting may therefore be involved in the development of the tools used in these confrontations, such as mandibles and stings.

Predictions: diploid social insects and vertebrates

For comparative purposes, it is worth considering the effects of imprinting in social diploids. These include some social insects, especially the termites, as well as cooperative species in taxa such as birds and mammals. The matrigenes-patrigenes asymmetries due to haplodiploidy will of course disappear, but those due to multiple mating or multiple reproductives may remain. Because both sexes are diploid, both could be imprinted. There are no longer any expected imprinting effects on the sex ratio favored by workers. Workers are equally related to the sexes within any kinship category, and they are therefore selected to favor a 50:50 sex ratio. More to the point, matrigenes and patrigenes agree on this, because they are symmetrically related to the two sexes of any given degree of relationship. This is true not only for close relationships, such as male and female full siblings, but also for more distant ones, such as male and female half siblings or cousins.

Because of this symmetry, we no longer need to consider effects on males and females separately in considering the evolution of competition affecting siblings. Here we have the classic imprinting case developed by Haig [5-8]. In species where social groups derive from single once-mated mothers, competition will exert a cost on full siblings, to which matrigenes and patrigenes are equally related, and no imprinting is expected. But when the mother mates

multiply, matrigenes are more related than patrigenes to the siblings affected, and matrigenes are therefore predicted to be less selfish. If, on the other hand, groups are headed by a male and multiple females mated to him, the predictions would be reversed.

Multiple reproductives have similar effects. If female reproductives are related to each other, but their mates are not, then matrigenes in their offspring should be less selfish than patrigenes. If male reproductives are related to each other, but females are not, patrigenes should be less selfish.

As in the haplodiploids, helping behavior is essentially the same problem as competitive behavior, but with the actor experiencing the cost and its colony mates experiencing the benefit. In the paragraphs above, "more selfish" and "less selfish" can be replaced by "less altruistic" and "more altruistic" respectively.

With diploids, there is nothing that exactly parallels the haplodiploid issue of whether workers should lay haploid male eggs, and whether other workers should police this behavior. However, we can ask whether workers should produce offspring (male or female) that would replace the queen's. In the absence of the haplodiploid sex asymmetries, this is a special case of competition with siblings, considered above. The only difference is that instead of considering effects on self and siblings, we are now considering effects on own offspring and effects on sib offspring. But this simply multiplies all relatednesses by $1/2$, leaving the b/c threshold unchanged. Therefore imprinting effects are as noted above. For example, there will be no imprinting effects with a single once-mated queen, and under multiple mating by a queen, matrigenes will be less selfish, in this case less prone to substitute their offspring for the queen's.

In diploids, policing of other worker's reproduction is not predicted to be imprinted. Workers are half as related to a full sibling's offspring as they are to the queen's offspring, so policing would generally be favored. This is equally true for matrigenes and patrigenes.

For discrimination in favor of one's own matriline or patriline, imprinting effects are still possible in diploids. Patrigenes will be more selected to promote their own patriline if there is a single queen mated to multiple males. The converse case, a single male mated to multiple females, did not seem relevant enough to discuss for haplodiploid social insects, but might be relevant to some cooperatively breeding vertebrates. Here matrigenes would be more selected to promote their own matrilines. Quantitative predictions will also depend, as in the haplodiploid case, on relatedness among the mothers and

fathers. Of course, whenever matrilines and patrilines within the group coincide, as among the progeny of a group of singly mated unrelated females, there should be no imprinting.

This discussion of diploids has been based on the assumption of autosomal gene control. Genes on the sex chromosomes may be selected differently. In particular, X-linked genes are predicted to evolve imprinting effects according to the haplodiploid pattern. Z-linked genes in birds would have similar predictions, but with male and female participants being interchanged because it is males that are diploid at such loci, while females are haploid.

Caveats

The attempt here to generate detailed testable predictions is of course not perfect. There are various reasons why the predictions could fail, even if the theory is correct, and it is worth pointing them out in advance.

First, all of the predictions are based on the assumption that social insects have the requisite tools to imprint genes and to express them differentially according to the parent of origin. Or to put it another way, a prior prediction is that they will indeed have evolved these tools because the theory predicts that they will be useful. But it is difficult to put much faith in this prediction unless the imprinting mechanisms are known to be very simple and easy to evolve. After all, one does not predict that wings will evolve in all organisms for which they would be useful, because wings are very complex.

Not every gene will be imprinted even in the predicted caste and tissues. In mammals, for example, placental genes are imprinted as expected from the theory, but only a select few. This may reflect a variety of causes. First, the relevant imprinting mutations may never have occurred at some genes. This seems particularly relevant if genes are imprinted in clusters [4] such that it is difficult to target one particular gene without hitting others. Second, not all placental genes directly affect the growth of the embryo in ways that can be modulated by an increase or decrease in expression due to imprinting. One possible cause is dominance. For a strictly dominant gene, reducing expression from one parent will have no effect on the phenotype.

For these reasons, the most decisive tests of the kin conflict theory are not which taxa will be imprinted or which specific genes will be imprinted. The best predictions concern those genes that do show imprinting. First, the functions of imprinted genes should be concentrated in the contexts describe above and not in other contexts. Second, the directions of the effects of matrigenes versus patrigenes should be as predicted.

The predictions have focused on differences in action thresholds for the matrigenes and patrigenes. When there is a difference, there will be a range of b/c values over which the matrigenes and patrigenes will favor different outcomes. However, in some circumstances, the actual b/c ratio will fall outside this range, and matrigenes and patrigenes will agree, at least qualitatively. For example, when daughter honey bee queens fight to the death over who will inherit the colony, patrigenes have the strongest interest in winning because they are probably not present in rivals, most of whom are half sisters. However, matrigenes also favor winning because the matrigene is definitely present in the queen in question, but has only a 50% chance of being present in the rival. So the patrigenes may favor winning if b/c exceeds a very small number, and the matrigenes if b/c exceeds $1/2$. But if one queen must win the colony and one must lose it, $b = c$ and the actual b/c is about 1, in which case both thresholds are satisfied. Conflict in this case would occur only if there is some additional cost, for example a risk of both queens being killed, that puts the b/c ratio in the conflict zone.

Tests of the prediction will of course need to confirm that the assumptions of the models hold. For example, I have generally assumed that queens produce the males rather than the workers. Workers production of males changes some of the relatednesses and also the sex-specific reproductive values of expression (expression 1). I have also made assumptions about who is affected by the behaviors in question. For example, the simple case to consider for worker laying of male eggs was replacement of the queen's sons. But, depending on what information workers have, they may not be able to do this perfectly. Worker laying may also sometimes end up replacing other workers' sons, worker-destined eggs, or even queen-destined eggs, and these would need to be added into the inclusive fitness analysis. The kinds of analyses done in this paper can easily be extended to such cases.

Power

One of the most interesting features of imprinting conflict, compared to most within-individual conflicts, is the even balance of power. Matrigenes and patrigenes are equally numerous (except on sex chromosomes) and can therefore lead to a deeply divided self. In contrast, a meiotic drive mutant that lowers fitness should be opposed by all other genes that are not tightly linked to it. The even match of the two parties under genomic imprinting makes the outcomes difficult to predict, although we can predict the different ends towards which matrigenes and patrigenes should strive. However, though matrigenes and patrigenes are equally numerous, it is only the imprinted ones that can pursue distinct strategies. Non-imprinted genes are usually selected to have a strategy intermediate

between those of the matrigenes and patrigenes, and their effects are likely to be important.

There are two factors that might give patrigenes an advantage in haplodiploids. First, maternal imprinting may be more constrained than paternal. If a father labels a gene in a way that changes its expression in his offspring, this affects only daughters, because he has no sons. When a mother labels a gene in this manner, her opportunities to conduct conflict in the diploid daughters may be constrained if the imprint also affects the fitness of her sons.

Patrigenes may gain a second advantage because the father's inclusive fitness interests are exactly the same as the patrigenic interests in the offspring, so there should never be any evolutionary conflict between the father's placing of an imprint and how the patrigene uses the imprint. In contrast, maternal inclusive fitness interests sometimes do not correspond exactly with matrigenic interests because of the intervening reduction division between mother and daughter. In single-queen colonies, the general rule is that maternal and matrigenic interests are different when the offspring's behavior affects its own fitness (Tables 2, 4, 6, 7). In contrast, there is agreement when the behavior does not affect that offspring, but instead affects a transfer of fitness between other individuals, as in the sex ratio, policing, or favoring one's own matriline or patriline (Tables 3, 5, 8, 9). In polygynous colonies, the fact that the queen can only imprint her own daughters is an additional source of differences.

In the special case of interactions among full sisters (Table 2, column 1), it is the patrigenes that actually match the maternal interests because the patrigenes are equally related to all sisters (including self), as is the mother. This would seem to provide a strong advantage to patrigenes. If patrigenes begin to evolve a novel expression pattern and gain an advantage, matrigenes might evolve a response, but they will get no help from mothers labeling genes in new ways. Indeed, one possibility is that mothers may evolve to thwart matrigenes by matching the paternal imprint, so that the matrigenes in their offspring will behave like patrigenes [20]. Of course, this matching would make this gene unimprinted, at which point it would begin to be selected according to maximize non-imprinted inclusive fitness. So this would push daughter behavior away from the optimal maternal/paternal/patrigene strategy. Now either parent might evolve an imprint if that has the immediate effect of diminishing daughter selfishness, but the matrigene can then evolve independently again. In other words, one possible result for full sister interactions is a co-evolutionary arms race alternating between imprinted and non-imprinted states.

The balance of power within individuals may also be affected by conflict between individuals. Within a female worker, patrigenes may favor female-biased sex ratios and matrigenes more even sex ratios. Left to themselves, they may be evenly matched, or the patrigenes may have some advantage owing to the constraints factor just discussed. But there is another party to the dispute. The queen also favors even sex ratios and her genes are not in conflict with each other. So selection on queens to influence sex ratios may give the matrigenes an advantage in their conflict with patrigenes, or to put it in the reverse orientation, the fact that workers have divided interests may give the queen an advantage in her conflict with workers. However, this advantage is clearly not overwhelming, as there is strong evidence that workers do create female-biased sex ratios in many species of haplodiploid social insects [24,42,50]. On the other hand, the queen sometimes does seem to win this conflict [51], despite the huge numerical advantage of workers, and the divided nature of workers could help explain why.

In the reverse direction, if the queen wins conflicts with her offspring, it will impact conflict within those offspring. In those conflicts where both patrigenes and matrigenes are selected to be more selfish than maternal genes (Tables 2, 4, 6, 7), when the population is at or near the maternal optimum, patrigenes and matrigenes are both being selected to oppose it, and are no longer in conflict with each other.

Conclusions

Evolutionary theories, like other scientific theories, make predictions about the world and they are judged on the success of those predictions. However, it is often difficult to construct truly novel predictions, predictions that are unbiased by what we already know about the real world. At one extreme, our "predictions" are not really predictions at all, but rather post hoc explanations of some known phenomenon.

Sociobiological theories have been accused of being particularly prone to this false kind of prediction, with theoretical explanations tailored to the facts already known [52]. While there are good reasons to dispute this characterization [53,54], it is true that it is unusual to find solid sociobiological predictions that are highly risky in the sense that nothing is known in advance about the empirical data. It is such risky predictions that, if verified, provide the most confidence in the underlying theory. A striking example is Richard Alexander's predictions about what a eusocial mammal would be like, if such a thing existed, strikingly confirmed by the discovery of eusociality in naked mole rats [55]. Even here, if the prediction had turned out to be false, it would not have caused a significant problem for sociobiological theory in general. It

would have falsified one researcher's rather idiosyncratic (but apparently correct!) views on factors important in the evolution of sociality.

Challenges to the larger framework are much more difficult to frame, but it is something along these lines that is attempted here. The theory of kin selection and the role of relatedness are central to sociobiological theory. Coupled with some new assumptions about genomic imprinting, kin selection theory makes some striking new predictions about within-genome selection on social insects, particularly those with haplodiploid genetic systems. As nothing is currently known about genomic imprinting in social insects, the predictions were derived in complete ignorance of what the result might be. As methods become available to study imprinting in social insects, the predictions can be tested.

If these predictions turn out to be successful, there will be two important consequences. First, the kinship theory of genomic imprinting will be greatly strengthened. It is difficult to imagine any other theory that would make the same set of predictions as those outlined here. By extension, such a result would confirm that we have a good understanding of how kin selection works in general. On the other hand, if imprinting and parent specific gene expression do occur, but the predicted patterns do not emerge, something must be wrong with the kinship theory of imprinting or kin selection theory in general.

Second, positive results would add another fascinating dimension to the nature of social insects. Most interest in social insects is generated by their extraordinary degree of cooperation, such that entire colonies often seem to function as single organisms. As such they may serve as good models for understanding other major evolutionary transitions in which separate individuals coalesce into a largely conflict-free unit [56,57]. If genomic imprinting has the predicted range of effects in social insects, they would also become outstanding examples of an opposite kind of selection, in which individuals are deeply divided by internal conflicts [13].

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