Genomic imprinting and kinship in the social Hymenoptera: What are the predictions?

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Abstract

The kinship theory of genomic imprinting predicts that conflicts of interest between parents can promote the evolution of opposed expression patterns of maternally and paternally derived alleles in the offspring. The social Hymenoptera (ants, some bees, and some wasps) are particularly suitable to test this theory, because a variety of social conflicts are predicted due to relatedness asymmetries between female and male nestmates that are a corollary of haplo-diploid sex determination. Here I argue that the kin-selection predictions for genomic imprinting in social Hymenoptera might in many cases be more complex than previously suggested, because the optimal strategy will have to take fitness effects in different castes and sexes into account.

1. Introduction

The genomes of diploid sexual organisms are divided into a maternally derived (“matrigenic”) part, and a paternally derived (“patrigenic”) part. Potential conflicts between these two parts arise when matrigenic and patrigenic genes are differentially related towards other individuals and therefore “disagree” on the optimal behaviour of the organism towards relatives. Therefore, the self-interests of parts of the genome can fraction the individual self of the organism (reviewed in Burt and Trivers, 2006). For example, in a species with a promiscuous mating system, patrigenes compared to matrigenes will favour more maternal investment into the embryo at a cost to the mother and maternal half-siblings, because they are not present in the mother or the other offspring. Matrigenes, on the other hand, are by definition also present in the mother and have a probability of 0.5 of also being present in siblings. Genomic imprinting has been interpreted in this kinship context (“the kinship theory of genomic imprinting” Haig, 2000; Haig and Westoby, 1989). Genomic imprinting is an epigenetic phenomenon, i.e. an imprint does not follow Mendelian inheritance, but instead can be replaced each generation. It occurs by parent-specific differential methylation of DNA or histone modification during gametogenesis, which can silence or upregulate the respective gene copy and thereby lead to parent-specific gene expression in the offspring (reviewed in Burt and Trivers, 2006). Imprinted genes are often involved in regulating embryonic growth and development and, as predicted by the kinship theory, paternally and maternally imprinted genes tend to increase and decrease growth, respectively (Burt and Trivers, 2006; Haig, 1992; Haig and Westoby, 1989).

Individuals in the societies of social Hymenoptera (ants, some bees, and some wasps) have close social interactions with related nestmates throughout development and adult life. At the same time, their haplo-diploid sex determination system (queens and workers are diploid females, males are haploid) frequently results in relatedness asymmetries between different classes of individuals and different parts of the genome. Furthermore, a large number of different social systems are present in different species, which leads to many different potential and actual social conflicts (Queller and Strassmann, 2002; Ratnieks et al., 2006). It has therefore been recognized that the kinship theory of genomic imprinting (Haig, 2000; Haig and Westoby, 1989) might particularly apply to the evolution of social behaviour in ants, bees, and wasps (Burt and Trivers, 2006; Haig, 1992; Queller, 2003; Queller and Strassmann, 2002). It has recently been suggested that “the haplo-diploid social insects offer the best opportunity to further test this theory” (Queller and Strassmann, 2002), and the underlying theory and predictions for social Hymenoptera have been developed in some detail (Queller, 2003).
So far there is no direct evidence as to whether genomic imprinting occurs in the social Hymenoptera. However, recent work has shown that the molecular machinery that underlies imprinting and DNA methylation in other organisms is present and functional in honeybees (Wang et al., 2006; Kronforst et al., 2008), and a variety of other ants, wasps, and bees (Kronforst et al., 2008). Furthermore, it has been demonstrated that DNA methylation in honeybees is used to store epigenetic information that determines whether a larva will develop into a worker or a queen (Kucharski et al., 2008). These findings set the stage for more in-depth studies of genomic imprinting in social insects, and potentially provide an array of novel tests of kin-selection theory. However, one important difference from diploid organisms without reproductive division of labour is that when the hypothetical genomic imprint is applied during gametogenesis in a social hymenopteran, there is in many cases an informational constraint as to whether the haploid genome will end up in a haploid male, a diploid queen, or a diploid worker. This means that at the moment where imprinting could take place, there is substantial uncertainty over what the optimal imprinting strategy should be. Because kin-selection predictions for genomic imprinting can be very different and often opposing for different castes and sexes (see the example below), overall predictions may be more complicated than suggested so far (Queller, 2003). For a given locus, predictions must take into account the expected fitness effects of imprinting for males, workers, and queens at the same time, as well as the relative probability of a gamete to end up in a male, a worker, or a queen. Here, I argue that further elaboration is necessary to be able to correctly interpret future empirical results from studies of imprinting and kinship in the social Hymenoptera.

2. Imprinting and kinship in the social Hymenoptera

The inclusive fitness effect for an allele can be calculated as follows: let the proportion of cases a given allele occurs over the generations as a maternally derived allele in workers be ($t_v$); as a maternally derived allele in queens ($t_q$); as a paternally derived allele in workers ($t_w$); as a paternally derived allele in queens ($t_p$); and as a maternally derived allele in males ($t_z$). These proportions will depend on the numerical sex ratio and the numerical queen to worker ratio in the population over time. Then, the allele’s inclusive fitness effect, $\delta W$, will be a weighted sum of its effect in each of these circumstances ($\delta W_v$, $\delta W_w$, $\delta W_q$, and $\delta W_z$, respectively):

$$\delta W = t_v \delta W_v + t_q \delta W_q + t_w \delta W_w + t_p \delta W_p + t_z \delta W_z$$

(1)

This equation assumes that a worker-derived allele has the same fitness function as a queen-derived allele in males. If necessary, an additional term could be introduced to allow these two functions to differ.

The similar case of X-linked inclusive fitness in diploid species has been dealt with by Haig (2000), and the formula given above for $\delta W$ is the equivalent of his formula for X-linked loci. Similar to his formulation of the invasion criteria for new alleles at X-linked loci, the invasion criteria for alleles at different types of loci in social Hymenoptera are given in Table 1.

An allele derived from a social hymenopteran queen should thus have an expression pattern that maximizes the inclusive fitness effect of the allele $\delta W_q$.

$$\delta W_q = p_v \delta W_v + p_w \delta W_w + p_p \delta W_p$$

(2)

where $p$ denotes the respective probability that the allele will end up in a certain caste or sex (the subscripts follow (1) above).

Similarly, an allele derived from a social hymenopteran male should be expressed to maximize $\delta W_m$.

$$\delta W_m = p_v \delta W_v + p_w \delta W_w + p_p \delta W_p$$

(3)

A worker-derived allele will only be expressed in a male ($p_x = 1$) and should simply maximize $\delta W_w$. Worker-derived alleles are therefore not subject to the same trade-off as queen-derived alleles. Note that, while $t$ represents an overall proportion over the generations, $p$ is a probability that applies to a given individual at a given point in time. Ultimately, $t$ will be a function of the amount of reproduction and $p$ at the time of reproduction, for all queens, males, and workers.

Again, this situation is somewhat reminiscent of imprinting on sex chromosomes in diploid species. Here, the imprint on a female-derived X chromosome has to be applied before it is decided whether this X chromosome will co-occur with a second X in a female, or with a Y in a male. Simple imprinting predictions can only be made for genes that are exclusively expressed in one sex.

As an example, I will consider the potential imprinting conflict discussed by Haig (1992) over the sex-investment ratio in single queen societies with singly mated queens. The logic can be extended to all potential conflicts discussed by Queller (2003).

<table>
<thead>
<tr>
<th>Type of locus</th>
<th>Expression</th>
<th>Mutant alleles favored if</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biallelic expression, not sex-limited, not caste-limited</td>
<td>${v, w, x, y, z}$</td>
<td>$t_v \delta W_v + t_w \delta W_w + t_p \delta W_p + t_q \delta W_q &gt; 0$</td>
</tr>
<tr>
<td>Biallelic expression, female-limited, not caste-limited</td>
<td>${v, w, x, y, 0}$</td>
<td>$t_v \delta W_v + t_w \delta W_w + t_p \delta W_p &gt; 0$</td>
</tr>
<tr>
<td>Biallelic expression, female-limited, queen-limited</td>
<td>${0, w, 0, 0, y}$</td>
<td>$t_v \delta W_v + t_w \delta W_w &gt; 0$</td>
</tr>
<tr>
<td>Biallelic expression, female-limited, worker-limited</td>
<td>${0, v, 0, 0, 0}$</td>
<td>$t_v \delta W_v + t_w \delta W_w &gt; 0$</td>
</tr>
<tr>
<td>Male-limited</td>
<td>${0, 0, 0, 0, z}$</td>
<td>$\delta W_z &gt; 0$</td>
</tr>
<tr>
<td>Maternally silent, not caste-limited</td>
<td>${0, 0, x, y, 0}$</td>
<td>$t_v \delta W_v + t_p \delta W_p &gt; 0$</td>
</tr>
<tr>
<td>Maternally silent, queen-limited</td>
<td>${0, 0, 0, y, 0}$</td>
<td>$\delta W_q &gt; 0$</td>
</tr>
<tr>
<td>Paternally silent, worker-limited</td>
<td>${v, w, x, 0, 0}$</td>
<td>$t_v \delta W_v + t_w \delta W_w + t_p \delta W_p &gt; 0$</td>
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</tr>
</tbody>
</table>

* An allele’s expression “strategy” is represented by $\{v, w, x, y, z\}$, where $v$ is the allele’s level of expression when maternally derived in workers; $w$ its expression when maternally derived in queens; $x$ its expression when paternally derived in workers; $y$ its expression when paternally derived in queens; and $z$ its expression when maternally derived in males.

* The proportion of cases an allele occurs in a given caste or sex over the generations is denoted by $t$, the inclusive fitness effect by $\delta W$ (see text for details).
The male perspective: At the time where an imprint could be applied on genes in a developing sperm, there is uncertainty over whether the genes will end up in a queen or a worker. If the sperm fertilizes an egg that develops into a new queen, the patrigenes in this queen favour equal investment in females and males (the queen's offspring), which is in line with the matrigenes' interest. No imprinting to counteract matrigenes effects is therefore favoured.

If the sperm fertilizes an egg that develops into a worker, the patrigenes in this worker favour investment only into females (the worker's siblings), which is in conflict with the patrigenes, which favour an investment of 1:1. Imprinting to strongly bias the investment ratio towards females is therefore favoured.

2.2. The worker perspective

At the time where an imprint could be applied on genes in a maturing oocyte, there is uncertainty over whether the imprinted genes will end up in a new queen, a worker, or a male. If the egg gets fertilized and develops into a new queen, the matrigenes favour equal investment in females and males (the new queen's offspring), which is in line with the patrigenes' interest. No imprinting to counteract patrigenes effects is therefore favoured.

If the egg gets fertilized and develops into a worker, the matrigenes favour equal investment in females and males (the worker's siblings). This is in conflict with the patrigenes, which favour investment only into females. Imprinting to counteract the effect of patrigenes and to increase investment in males is therefore selectively favoured.

If the egg does not get fertilized and develops into a haploid male, by default there are no conflicts between matrigenes and patrigenes, because males lack patrigenes. Expression patterns should therefore maximize male inclusive fitness.

2.2. The worker perspective

Worker-laid eggs can only develop into haploid males, so that gene expression patterns should simply maximize male inclusive fitness.

3. Discussion

Although data is still sparse, it has become clear that genes that are expressed in social insect workers vs. queens overlap substantially (e.g. Hoffman and Goodisman, 2007). In the context described above for the conflict over the sex-investment ratio, these may be genes that influence behaviours such as the killing of male larvae, the regulation of and response to larval food begging, feedback between larvae, mother queen, and workers via larval regurgitates, but also developmental genes. For these genes, there is no simple prediction for the optimal expression and, therefore, the optimal imprinting strategy at the egg or sperm stage, if the predictions are different depending on whether the genes end up in a worker or a queen. Analogously, it is not clear to what extent genes that affect worker and queen development and behaviour will affect male development and behaviour. But again, it seems reasonable to assume that many genes are similarly expressed in males and females (Hoffman and Goodisman, 2007). In such cases, epigenetic effects on expression could, for example, be detrimental to the development of haploid males (Queller, 2003). One testable prediction of such a scenario would be that epigenetic regulation patterns for some genes might differ between worker- and queen-derived males. As has been outlined above, maternal effects in worker-derived males should simply maximize male inclusive fitness, while maternal effects in queen-derived males should reflect a trade-off between male, worker, and queen inclusive fitness.

On the other hand, the original predictions with respect to imprinting by Queller (2003) will apply to genes that are only expressed in a single caste and/or a single sex, and to genes that are regulated by different mechanisms in different contexts. The former is known for a number of genes, and many genes show caste and/or sex-specific expression levels (e.g. Hoffman and Goodisman, 2007). The latter could, for example, be implemented by having alternative promoters which regulate gene expression in workers, queens, and males, respectively, or generally by alternative methylation sites. A context-dependent specific imprinting strategy could then apply to each of these promoters or sites. This scenario seems plausible, because tissue-specific transcription from imprinted loci has indeed been shown to be regulated from alternative promoters (e.g. Valleley et al., 2007). Furthermore, genes could have different functions in males, queens, and workers, and these functions do not necessarily have to be related to the same kin-conflict. If we consider the above given case of sex-investment conflict, for example, the genes that are involved in determining the sex-investment ratio might be different in queens and workers. Queens determine the primary sex-investment ratio, i.e. the ratio of female to male eggs laid, but the extent to which they control the secondary sex-investment ratio, i.e. the energy that is invested into female and male offspring throughout the development, varies between species and may be quite limited in some cases. Workers, on the other hand, primarily exert control over the secondary sex-investment ratio, although they are capable of producing male eggs in many species (Ratnieks et al., 2006). The mechanisms, and probably also the genes involved, therefore, at least partially differ between queens and workers. Although imprinting of a locus that has different functions in queens, workers, and males may still affect all castes and sexes as has been described above, we would then merely be faced with the general problem of adaptive evolution under pleiotropy.

Social insects have the potential to provide a variety of fruitful tests of the kinship theory of genomic imprinting (Haig, 2000; Kronforst et al., 2008; Queller, 2003; Queller and Strassmann, 2002). Empirical studies now have to show whether kin-selected imprinting and gene expression patterns occur in the social Hymenoptera, and to what extent these patterns follow simple (cf. Queller, 2003) or more complex “strategies”.

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References