The emerging study of kinship theory in the honeybee, *Apis mellifera*

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The social structure of bee colonies presents an evolutionary conundrum: how could an entire caste of sterile, cooperative worker bees exist when natural selection dictates that individuals must outcompete others in producing offspring in order to pass on their characteristics? Described as “one special difficulty” for his theory by Charles Darwin himself, it was not until over a century after the publication of The Origin of Species that this question could be addressed with a modern understanding of genetics.

The solution, called kin selection theory, resolves the issue of worker bee sterility by including not only an individual’s offspring in the calculation of its fitness but also the survival and reproduction of the individual’s relatives. In this way, one accounts for the total number of genes propagated by an individual, cultivated both directly (by reproducing) and indirectly (by helping relatives). Kin selection theory thus explains altruistic behavior as a function of improving one’s own genetic legacy, or why some individuals help others at a personal cost: their genes win out in the bargain. One may even calculate how many relatives outweigh your own reproductive potential from how closely related you are to your beneficiaries, or as one geneticist once quipped, “I would lay down my life for two brothers, or eight cousins.”

Honeybees will certainly lay down their lives for dozens of relatives, as illustrated by their selfsacrificing stingers. It is the worker bees of the hive that engage in this behavior in addition to foregoing reproduction in favor of helping to raise their sisters. There is one more important observation here: all worker bees are female. Female honeybees are much more closely related to their sisters, sharing 75% of their DNA, than they are to their progeny, who only inherit half of their mother’s genes. Therefore, female honeybees on the whole favor helping their sisters over-producing their own offspring. Conversely, male honeybees share their DNA disproportionately with their offspring, passing on their full set of genes to their daughters while only sharing half of their genes with their siblings. Since altruistic behavior is contingent upon the genetic similarity between individuals, the observed difference between the sexes in reproductive behavior, with all males preferring to reproduce and most females preferring to raise sisters, is expected.

In 2003, David Queller predicted that this difference in strategies between the sexes of maximizing their fitness also manifests within an individual honeybee’s genome, an idea he called kinship theory. The worker bees have different fathers but all have the same mother: the queen of the hive. Therefore, the genes from the mother would favor helping the individual’s sisters, while the genes from the father would only benefit from reproduction. This conflict is the logical continuation of the previous discussion of kin selection theory and yet deeply counterintuitive. How could the genes of one individual be in conflict with each other?

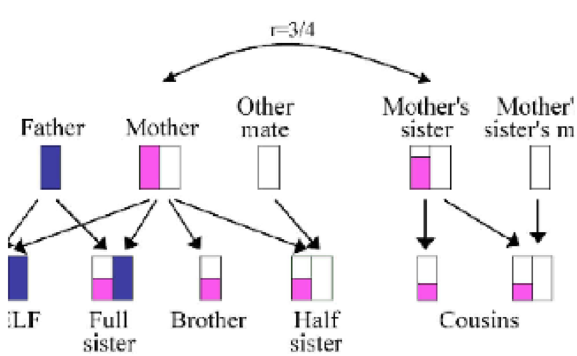

Figure 1. Distribution of an individual worker bee’s genes inherited from her mother (pink) and father (blue). Note that only maternally-inherited genes benefit from altruistic behavior toward brothers, half sisters, and cousins. Reprinted from Queller 2003.

One must imagine the gene as “acting” in favor of only its own reproduction. Therefore, it is possible that maternal and paternal genes compete to increase their number of copies at the expense of the other parent’s genes’ survival within the population. In fact, there exists a molecular process for mediating this competition called genomic imprinting. This process can occur via DNA methylation such that the version of a gene from one parent is silenced, resulting in the exclusive expression of the other parent’s version of that gene. When Queller theorized the conflict between the reproductive interests of the maternal and paternal genes within individual honeybees, it had not yet been established that honeybees were capable of DNA methylation. It has since been shown that honeybees do have a gene methylation system and the modulation of DNA in this way has now been associated with changes in the development and activity of bees’ ovaries. Therefore, bees are capable of the molecular process that can facilitate genomic imprinting, and there is strong theory to suggest there is selective silencing of genes based on the sex-specific patterns of inheritance and behavior in the honeybee.

A recent collaborative effort between Queller and other scientists tested kinship theory by cross-breeding Africanized and European worker bees. The researchers already knew that Africanized honeybees develop larger ovaries and produce more eggs than their European counterparts. Therefore, they predicted that the hybrid worker bees with Africanized fathers and European mothers would develop larger ovaries and produce more eggs than the bees with European fathers and Africanized mothers based on the hypothesis that the father’s genes would increase the growth and activity of these reproductive organs. The results were as predicted: the bees with Africanized fathers had larger ovaries and reproduced more than those with Africanized mothers, suggesting that the father’s genes do increase reproduction as compared to the mother’s genes.

The study also took advantage of RNA sequencing technology to compare the expression of maternal and paternal genes between sterile and reproducing worker bees. Again, as expected, reproducing bees expressed the paternal versions of genes over the maternal versions more often than sterile bees. Additionally, several of these differentially-expressed genes are known to be involved in egg production, such as the transcription and upregulation of an important yolk precursor protein.

These results support the theory that maternally and paternally inherited genes compete to determine the reproductive behavior of worker bees with expression of paternal genes favoring increased reproductive behavior as compared to the maternal versions. These findings also provide strong support for kinship theory since the study conclusively demonstrated that paternally-inherited genes favor behaviors that increase reproductive behavior while maternally-inherited genes favor altruistic behaviors. The social insect has always been a valuable subject for the study of kin selection and these results suggest a promising new opportunity for investigation of this theory within the genome.

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