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Gene wars across the generations permlink

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Posted on: September 14, 2009 8:36 AM, by Razib Khan

Nearly 50 years ago W. D. Hamilton published two papers, The genetical evolution of social behaviour - I & The genetical evolution of social behaviour - II, which helped revolutionize our conception of how social and genetic process might work in concert. It opened up a field of research which was highlighted in Richard Dawkins' The Selfish Gene, and helped make inclusive fitness a general idea which allows us to view specific phenomena through a powerful theoretical lens. Hamilton's original work was broad in its implications and abstract in method, but concretely utilized various eusocial insects as biological illustrations, and in particular the hymenoptera, which are characterized by haplodiploid sex-determination.

In a haplodiploid scenario the males, the drones, are haploid. They have half the number of chromosomes as females, workers or queens, who are diploid. They receive all these chromosomes from their mother, and no genetic input from fathers. That is, drones are the products of unfertilized eggs. Females are the products of fertilized eggs, but if (as is often the case) only one male mates with the queen, then **sisters will have a coefficient of relatedness with each other of 3/4, because all the genes they receive from their father will be identical.** This is because he is haploid, and so contributes his total genome content to his daughters (as opposed to 50% as would be the case if he were diploid). In contrast, the mother contributes half her genome, and so there is an expectation that sisters will share only half their distinctive genes from their mother. 50% identical + 1/2 * 50% = 75% identical.

When Hamilton and his coworkers (John Maynard Smith was working in the same area of mathematical evolutionary biology, while George Williams was tearing down group selection) developed their theories genetic relatedness among hymenoptera was assumed. But with cheaper genotyping technologies over the decades evolutionary biologists have been able to look much closer in regards to the genetic structure of a colony. The reality is more complex than Hamilton's assumptions, and the colonies of eusocial insects are often diverse when it comes to relatedness. In some cases it turns out that relatedness is far less than 3/4, and that cooperation occurs even when it is below the critical threshold given by Hamilton's Rule. In other cases, there are a variety of morphs which operate in competition and cooperation in a facultative manner (sound familiar?). Some of the complexities have resulted in the emergence of group (colony) selection models to explain how unselfish behavior can persist despite the lack of the inclusive fitness context.

Hymenoptera are themselves diverse, exploring a variety of ecological niches and characterized by a range of behaviors and colony structures. A recent group has published a paper exploring (or uncovering) long term persistence of distinct lineages within a colony, The queen is dead--long live the workers: intraspecific parasitism by workers in the stingless bee *Melipona scutellaris*:

> Insect societies are well known for their high degree of cooperation, but their colonies can potentially be exploited by reproductive workers who lay unfertilized, male eggs, rather than work for the good of the colony. Recently, it has also been discovered that workers in bumblebees and Asian honeybees can succeed in entering and parasitizing unrelated colonies to produce their own male offspring. The aim of this study was to investigate whether such intraspecific worker parasitism might also occur in stingless bees, another group of highly social bees. Based on a large-scale genetic study of the species Melipona scutellaris, and the genotyping of nearly 600 males from 45 colonies, **we show that ~20% of all males are workers' sons, but that around 80% of these had genotypes that were incompatible with them being the sons of workers of the resident queen.** By tracking colonies over multiple generations, we show that these males were not produced by drifted workers, but rather by workers that were the offspring of a previous, superseded queen. This means that uniquely, workers reproductively parasitize the next-generation workforce. Our results are surprising given that most colonies were sampled many months after the previous queen had died and that workers normally only have a life expectancy of ∼30 days. It also implies that reproductive workers greatly outlive all other workers. We explain our results in the context of kin selection theory, and the fact that it pays workers more from exploiting the colony if costs are carried by less related individuals.

They sampled colonies over several years, and even managed to genotype several queens. It turns out that the genotypes of the drones who were atypical (that is, they're not from the current queen and so are not as closely to the majority of the workers) weren't so varied as one might expect from a small but diverse number of alien workers. Rather, the genotypes of the drones implied that the mothers were the daughters of previous queens! The authors note that the expectation is that workers live about 30 days, but that timing of the sampling suggested that some of the "previous generation" workers who were reproducing so to give rise to these drones were living at in excess of 100 days (which is when the previous queen had died, and so must be a peg which fixes the youngest of previous generation workers).

How could this occur? One hypothesis is that these older generation workers simply shirked their workerly duties, did not expend energy, or take risks which would increase their mortality. There are strong genetic incentives for workers who are closely related to not shirk their duties (though even they sometimes engage in selfish behavior and lay eggs, though this is generally "policed"), but for workers who are more distantly related to most of the hive there is a rational opening for parasitizing and free riding on the behavior of the colony. Shirking duties and focusing on reproduction comes at the cost of the maintenance of the colony, but if the colony is genetically rather dissimilar than the "loss" via inclusive fitness because of colonial degradation or risk of collapse are sharply reduced. The authors note that it is possible that these reproducing older workers live as long as queens, and it seems to me that what they've really discovered is an alternative behavioral morph in this species of bee. These sorts of phenomena are not limited to hymenoptera, in Demonic Males the authors report that there are two types of male orangutans, large slow ones to whom females are attracted to, and small fast ones which have to catch and rape female orangutans to reproduce.

Over the years that W. D. Hamilton's original insights and framework have turned out to just be the beginning. Social insects might not be as intelligent as humans, but the complexity of their behaviors and the subtly of their societies may surprise us yet. A through empirical mapping of their behavioral ecology may lead us to new theoretical frameworks. After all, if the adaptive landscape was characterized by a simple topology, why are there so many species?

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Comments

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There is a small typo about orang-utans, you probably mean « small fast ones » (not « slow fast »).

Posted by: Jérôme ^ | September 14, 2009 10:09 AM

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