Ignorance is sometimes bliss

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In honeybee colonies, bees do not distinguish between siblings and half-siblings. If genetic relatedness were the only thing that matteree, they would be more helpful to bees that carry more of their genes. But the colony operates under a "veil of ignorance" that prevents them from making these distinctions and preserves group harmony. This makes evolutionary sense because it is costs and benefits impact evolutionary success as well as relatedness. Credit: WAUSBERG

A range of examples suggests a lack of information about their fellows can favor cooperation and prevent conflict among animals—and even among genes.

For the Oct. 16 issue of *Biology Letters*, a special issue commemorating the 50th anniversary of W.D. Hamilton's famous paper on kin selection, two Washington University in St. Louis biologists contributed an article describing intriguing exceptions to one of his predictions.

The basic idea of natural selection is to pass on your genes, but Hamilton pointed out, in an article that revolutionized the study of social evolution, that you can pass on genes by helping your relatives as well as your offspring.

Hamilton predicted that organisms ought to evolve the ability to discriminate degrees of kinship more and more finely. Genes that made them choosy would survive to future generations because they would direct help to those individuals with whom they shared the most genes.

True, say evolutionary biologists David Queller, PhD, the Spencer T. Olin Professor of Biology in Arts & Sciences, and Joan Strassmann, PhD, the Charles Rebstock professor of biology, but there also seem to be many cases where "a veil of ignorance" prevents organisms from gaining this kind of information. That forces them to consider a situation from the perspective of all members of their group instead of solely from their own perspective or that of their close kin.

In this way, the veil of ignorance can favor cooperation and suppress conflict within groups. The question, the scientists say, is whether ignorance is selected as a trait because it favors group harmony or merely persists once it evolves because it helps foster cooperation.

Lowering the veil

"A curious finding that arose from work with social insects, some our work and some by others, is that although social insects are pretty good at recognizing foreigners from a different colony they seem almost

universally bad at distinguishing among different degrees of relatedness within their own colony," Queller said.

"In many colonies, this doesn't matter because all of the insects are the progeny of a single mother, so they're all full sisters. But in others, such as honeybee colonies, the queen mates with multiple males, and so there are 17 or 20 sets of paternal genes, which we call patrilines, within the colony. The insects are half sibs; they all share the same mother but they have different fathers," he said.

"The bees don't distinguish among half and full sisters and nobody knows why for sure. So this is an example of a veil of ignorance," Queller said. "It works to the advantage of the colony because if the bees can't tell half and full sisters, they'll be out foraging rather than loitering near the queen cells to make sure a full sister becomes the next queen," he said.

The bees apparently recognize one another by means of distinctive hydrocarbons in their cuticles, or exoskeleton. If a worker bee is isolated, it will develop a distinctive hydrocarbon profile and be rejected if it is reintroduced into a colony.

But within the colony, the hydrocarbons rub off on other bees and on nest material as the bees feed, groom and move about, so that the hydrocarbons get mixed together, creating a general colony odor.

The question, said Queller, is: Why did cues that rub off evolve in the first place? "It's possible they evolved to mask kinship within colonies because kin-blindness benefits the colony. But it's also possible that the veil of ignorance arose for other reasons, and it's just that once it did arise, it was retained because it helps to cement group function and cooperation," he said.

The scientists describe two types of veils in their article. One is ignorance of relatedness, but the second is ignorance of payoffs. The social amoeba Dictyostelium discoideum illustrates the second type of veil. Groups of amoebas join together to form fruiting bodies; amoebas that end up in the stalk die and do not pass on their genes, but at the time they aggregate (above), the amoebas may be ignorant of their status relative to other amoeba and their likelihood of ending up in the stalk. Credit: STRASSMANN

The work on the within-colony veil of ignorance has additional implications for the practice of science, said Strassmann. "One is that it shows the danger of oversimplication. Hamilton's famous kin-selection inequality takes into account both the relatedness of cooperators and the costs and benefits of cooperation. Because relatedness is easier to measure, the costs and benefits can get ignored. Within-colony kin blindess is one example that shows how the benefits of cooperation can trump fine gradations of genetic relatedness," she said.

The second implication, she said, "is that it is important to understand the mechanism that underlies an evolved trait. If being able to discriminate among degrees of kinship within a colony were an

advantage, the mechanism for recognition would not be shared across colonies," she said.

"Our understanding of adaptation advances best with a clear understanding of both evolutionary advantage and mechanisms," she said.

Lifting the veil

Hamilton predicted that kin recognition might reach all the way down to genes. He said it was possible that one gene might be able to detect other organisms carrying a copy of itself.

He was right. The red fire ant, for example, has a gene that worker offspring can recognize and workers with this gene kill all queens that don't have it.

Genes like this one are called greenbeards, because they confer an externally visible label that allows them to spot copies of themselves, much as if every man with this gene dyed his beard green.

But what about the mother's genes and the father's genes in an embryo? These long have been thought to lack self-identity and to be shrouded under their own veil of ignorance so both sets of genes work for the common good.

We now know that some genes are marked as maternal or paternal through the addition of methyl groups while they are in the egg or sperm.

As a result of marking, called imprinting, the veil of ignorance lifts. "Considerable evidence suggests that imprinting leads to conflict between the matrigenes and the patrigenes in the embryo," Queller said.

The milkweed tussock caterpillar provides another example of ignorance of payoff. Its bright colors warn predators that it is toxic, having taken on poisons by feeding on milkweed and dogbane. A caterpillar may die if she attracts a naive predator and if she knew in advance that she would be a teaching example she might opt for less conspicuous colors. But since she cannot know, selection favors bright colors that deter experienced predators. Credit: STRASSMANN

A mouse, for example, can mate with more than one male and have a litter with two or more fathers. It's in the interest of the father's genes to produce large offspring that compete for maternal resources at the expense of other pups. And it's in the interest of the mother's genes that all of her offspring survive to adulthood so they, too, can reproduce.

Not surprisingly, many of the genes that are imprinted are somehow involved in growth and metabolism. "The father's trying to crank up something that causes the offspring to get more, and the mother's trying

to crank down the very same thing," Queller said.

Does this have anything to do with social justice?

The phrase "veil of ignorance" is not original to biology. It comes from a long tradition of thinking about the social contract in human societies.

Philosopher John Rawls, for example, suggested the veil of ignorance could be used in a hypothetical scenario in which a group of people is deciding the political and economic structure of that society. Each person is ignorant of his or her gender, race, age, intelligence, wealth, skills, education and religion. The idea is this device will force them to make choices that benefit all members of society, including the least advantaged.

Asked if there is a connection, Queller said, "This is not a matter of the social contract; it's a matter of biology. But sometimes, biological individuals or groups are able to arrive at something that resembles a social contract. They don't do it consciously, but sometimes it works out that way."

But he then gives an example where the veil of ignorance produces injustice. Slave-making ants, he said, have lost the ability to care for their young and themselves. To survive, they raid the nests of other ants and steal the pupae. Once the pupae emerge, they imprint on the colony odor and work as if they were members of that colony. "That's a veil of ignorance, but it doesn't lead to justice in any sense," Queller said.

Nonetheless, Queller and Strasmann's examples are thought-provoking, particularly in the age of the Internet, which enables blind interactions among individuals whose true identities are concealed.