VIEWPOINT

The Many Selves of Social Insects

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Social insects show multiple levels of self identity. Most individuals are sterile workers who selflessly labor for their colony, which is often viewed as a superorganism. The superorganism protects itself with colony recognition systems based on learned odors, typically cuticular hydrocarbons. Transfer of these odors within the colony obscures separate clan identities. Residual individual interests do appear to cause conflicts within colonies over sex ratio, male production, caste, and reproductive dominance. However, genomic imprinting theory predicts that the individual's maternal and paternal genes will evolve separate infraorganismal identities, perhaps leaving virtually no coherent individual identity.

Social insects have many selves in the sense that they live in colonies with many individuals. More interesting, they display multiple levels of self. For evolutionary biologists, the self is the individual, the unit that is coherently selected to nourish itself, to protect itself, and especially to reproduce itself. This unit is not fixed. Some individuals are simple prokaryotic cells, others are eukaryotic cells that originated as small communities of prokaryotes, and others are multicellular populations of eukaryotic units (*1*). Each higher level is granted individuality or selfhood when its constituents evolve to merge their separate identities and to work together with little or no conflict.

The social insects, which include termites, ants, some bees and wasps (Fig. 1), and a few others, take the progression one step further. At least in more highly developed forms, social insect colonies are so tightly integrated that they seem to function as single organisms, as a new level of self (*2–4*). The honeybees' celebrated dance about food location is just one instance of how their colonies integrate and act on information that no single individual possesses (*3*). Their unity of purpose is underscored by the heroism of workers, whose suicidal stinging attacks protect the single reproducing queen.

In addition to the shift to a higher-level self, we suggest that there has also been a shift in the opposite direction. Genomic imprinting may result in a fractured self in which maternal and paternal subsets of genes in an individual acquire their own identities and work at cross purposes with each other. The forging of both superorganismal and infraorganismal levels depends crucially on informational cues that define the new selves.

The Colonial Self: Superorganismal Identity

The transformation to superorganismal colonies was effected by kin selection (*5–7*). The genes for any trait of sterile workers, including sterility itself, are transmitted indirectly through reproducing relatives (relatedness measures the degree to which iindividuals share genes above random expectation). It is therefore essential that the fruits of worker labor not be directed toward nonrelatives. Foreign workers might enter a colony to steal its resources, or foreign queens may try to usurp the colony and substitute their own offspring for those of the resident queen. Most social insects have well-defined colony boundaries with few entrances, and they attack foreigners who broach those boundaries. However, simple exclusion is insufficient for discontinuous superorganisms that send out pieces of themselves to find food. They need to recognize and readmit these pieces without admitting intruders.

The cues that signal colony membership are chemical and can be either genetic or environmental in origin (*8–11*). Self versus nonself differs for each colony, so the cues must be learned, in contrast to the consistent cues that distinguish male from female or queen from worker (*12*). When an individual is born into her own colony, she is surrounded by the odors of colonymates and nest material, so she can learn these cues as a template for later reference in less certain contexts (*8–11*, *13*, *14*). Considerable evidence suggests that hydrocarbons in the cuticle are important in the colony odor (*9–11*). For example, *Cataglyphis niger* ants treated with hydrocarbon extracts of non-nestmates became less acceptable to their own colony and more acceptable to the hydrocarbon donor colony (*15*). The addition of synthetic hydrocarbons to paper wasps implicated alkenes and methyl-branched alkanes (*16*). Honey bees also use cuticular compounds, but fatty acids appear to be more important than hydrocarbons (*8*).

Fig. 1. An example of a superorganism, a colony of the wasp *Apoica albimacula*. This unusual nocturnal species has an open nest, defended by fierce stinging behavior, with warning given by the red worker abdomens, often arrayed in neat rows. [Photo by Horacio Paz, identification by Kurt Pickett]

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The Individual Self

Whenever there is more than one mother or father contributing to a colony, a worker could gain by favoring members of her own genetic clan, even at some cost to colony function. For example, any honeybee worker who stayed near the queen cells and ensured that the new queen was her full sister [relatedness (r) = 3/4] rather than a half sister (r = 1/4) would gain far more genetically than she would lose by not foraging for the colony. Yet clan nepotism appears not to happen (*17*). Instead, there seems to be a "veil of ignorance" (*18*, *19*) cloaking clan identity, forcing individuals to behave for the greater good. This is puzzling, because all that is required for clan recognition is for the individual to learn her own odor cues as a template, instead of the colony's cues, and to favor colonymates who most resemble this template. The veil of ignorance is woven by the shuttling of cues across the colony. Though produced by individuals, cuticular cues are spread among them by feeding, grooming, and contact with nest materials (*8*, *10*, *20*). But why should an individual acquiesce in the masking of her own clan identity when it would reduce nepotism from her own clan? Masking might actually increase aid from other clans (*21*), or it could reduce her chance of being mistaken for a non-colonymate. Workers isolated from contact can acquire distinctive hydrocarbon profiles and face rejection on reintroduction to their colony (*22*, *23*).

Though colonies generally seem to function as superorganisms, there remain areas in which separate individual interests can cause conflicts within colonies. These are best studied in the hymenopteran ants, bees, and wasps; to understand them, it is necessary to consider the strange relatedness patterns generated by their haplodiploid genetic system, in which fertilized eggs yield diploid females and unfertilized eggs yield haploid males (Fig. 2). For example, the female workers are more related to their full sisters (r = 3/4) than to their brothers (r = 1/4), so they are predicted to try to invest three times as much in rearing the former (*24*). Meanwhile the queen, who is equally related to her daughters and sons (r = 1/2) is selected to favor equal investment (*24*). Numerous studies now show that workers, who have a numerical advantage over the queen and do all the brood care, successfully produce female-biased sex ratios (*25*), although in some species queens may win the conflict (*26*). Such discrimination requires only that workers distinguish male from female colonymates, so a veil of ignorance is harder to impose, though males might evolve to mimic the more favored females (*27*).

Workers in many species, though unmated, can still potentially produce sons. Other things being equal, a worker should prefer to replace the queen's sons (her brothers, r = 1/4) with her own sons (r = 1/2) (Fig. 2). Other workers may oppose this when the queen is multiply mated so that workers are half sisters, preferring their brothers (r = 1/4) to nephews (r = 1/8) (*28*). The higher bees fit the expectation well; in multiply mated honeybees, workers eat each other's eggs (*29*), whereas in the singly mated stingless bees, workers often (though not always) successfully produce males (*30*). Workers in singly mated bees and wasps may even kill the queen near the end of the season so that they can produce their own males (*31*).

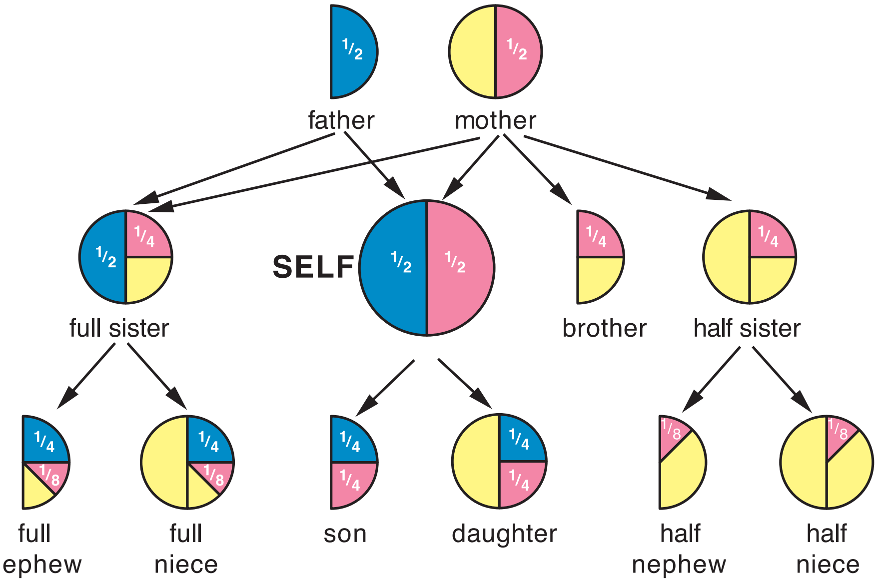

Fig. 2. Haplodiploid pedigree and relatedness. Females are diploid and shown by complete circles. Males are haploid half-circles. Relationships are for the large diploid female individual in the center, labeled "SELF". Her matrigene (pink) and patrigene (blue) derive from the mother and father, respectively, and their expected presence in other relatives is shown by the pink and blue areas. Unrelated genes are shown in yellow. SELF's relatedness to another individual is the summed pink matrigenic (m) and blue patrigenic (p) areas of the other individual. Thus, for a full sister, the relatedness is 3/4: p = 1/2 from the patrigene, and m = 1/4 from the matrigene. (These are life-for-life coefficients, rather than regression coefficients, because they include the twofold greater reproductive value of females.) To minimize clutter, unrelated male mates (who contribute yellow half-circles to daughters) are not shown.

The costs of within-colony conflicts can be high. In stingless bees of the genus *Melipona*, around 20% of female adults are morphological queens. Nearly all of these are killed by workers because they do no work and only the occasional new queen is needed to replace a failing queen or to head a reproductive swarm. This enormous waste of excess queens makes sense given that queens and workers are fed identically in *Melipona*, so that each female can determine her own caste (*32*). Models show that the high payoff of gaining a colony of one's own offspring (r = 1/2) rather than letting a sister win (r = 3/8) makes it pay for around 20% to enter the long-shot queen sweepstakes (*33*). This costly competition is avoided in species where workers control the caste of brood by differential feeding, as in honeybees. Even so, one or a few superfluous honeybee queens are often produced, and these fight to the death for right to head the colony.

The Fractured Self: Infraorganismal Identity

Despite appearances, the individual self is not always perfectly cohesive. When different parts of the genome can be transmitted in different ways, selection can lead to within-individual conflict. Thus, genes may be selected to get into more than their share of gametes, to copy themselves into other chromosomes, or to bias the sex ratio if they are transmitted more through only one sex (*34*, *35*). An unusual example in social insects comes from the fire ant, *Solenopsis invicta*, in which workers bearing one allele kill queens who lack it (*36*). Often such conflicts are minimized by power asymmetries, particularly of the many-against-one kind (*35*, *37*). A meiotic drive mutant that reduces fitness should be opposed by all other unlinked genes, and a maternally transmitted organellar gene may be outvoted by the more numerous biparentally transmitted nuclear genes.

More equally matched conflicts might occur between the maternal and paternal halves of the genome, but these have long been thought to lack self identity, shrouded under their own veil of ignorance. If genes cannot identify themselves as maternal or paternal, they can do no better than to act for the common good of both. However, recent work shows that genes can be differentially marked in parents, or imprinted, usually by methylation (*38*). As a result, the veil of ignorance is lifted, and the maternally and paternally derived genes in the offspring—let's call them matrigenes and patrigenes—can behave differently and can be selected differently. Haig has argued that such imprinting effects evolve when the matrigenes and patrigenes have different kin-selected interests, chiefly when the offspring is drawing resources from the mother (*39–41*). An offspring's matrigenes are closely related to all the mother's other offspring, so they do best not to harm the mother's future reproduction too much. However, an offspring's patrigenes are unrelated to any of the mother's other offspring who have a different father, so they will be more selected to drain the mother for their own benefit. This theory seems to account for why imprinted genes are concentrated in organisms with parental care (plants and mammals), why they are often expressed in embryos or embryo surrogates such as placentas and endosperms, and why patrigenes typically promote embryo growth, whereas matrigenes tend to suppress it (*41*, *42*).

We suggest that the haplodiploid social insects offer the best opportunity to further test this theory. Lifting the veil of ignorance from matrigenes and patrigenes should have many consequences. One reason is that haplodiploidy generates novel kinds of relatedness asymmetries (*43*), which can be traced in Fig. 2 for matrigenes (m = pink area) and patrigenes (p = blue area). In the simplest case, a female's patrigene makes up half of her full sister ($p = 1/2$) but is absent in her brother ($p = 0$), whereas her matrigene has an equal presence in both ($m = 1/4$). As Haig pointed out, this should lead to imprinting effects on worker sex ratio: Paternal genes should be selected to favor rearing sisters, and maternal genes should be more even-handed (*43*).

Social insects also provide great scope for imprinting conflict because they have such a wide array of interactions with relatives. Haig suggested that imprinting would affect a female's fundamental social choice between reproducing and helping a mother to reproduce (*43*). This makes sense for raising sisters instead of daughters, but not when we take into account that she would be raising both sisters and brothers [average $p = 1/4$, average $m = 1/4$ (Fig. 2)]. Still, the general idea has many other applications. Should a worker replace her mother's male egg ($p = 0$, $m = 1/4$) with her own? Patrigenes should favor this more than matrigenes. Should another worker remove this nephew-to-be ($p = 1/4$, $m = 1/8$) to allow only brothers ($p = 0$, $m = 1/4$)? Matrigenes will favor it more than patrigenes. Should a *Melipona* female enter the queen sweepstakes to produce her own offspring ($p = 1/4$, $m = 1/4$) or allow one of her sisters to do so ($p = 1/4$, $m = 1/8$)? Her matrigenes should favor competing in the sweepstakes more than her patrigenes. Imprinting could also affect kin recognition; the absence of clan discrimination makes more sense if matrigenes evolve to oppose discrimination among paternal clans (*21*).

Competition among rival queens is also expected to be imprinted (*42*), with predictions that depend neatly on the genetic structure. When queens are full sisters, as is common in *Polistes* paper wasps, matrigenes should be selected to compete harder than patrigenes. When they are half sisters, as in honeybees, the prediction is reversed. And when they are unrelated, as in most ant co-foundresses, there is no asymmetry and there are no predicted imprinting effects.

Because imprinting is predicted for different contexts than the standard offspring growth one, we expect imprinting in different tissues. Most of the conflicts are over adult reproduction and would involve ovaries, nervous tissues, exocrine glands, sensory organs, and perhaps weapons or other determinants of strength. In groups such as *Melipona*, genes affecting queen-worker determination would also be involved.

Currently, we do not know if social Hymenopterans have imprinted genes, let alone whether any imprinted genes have been selected to create infraorganismal identities. This provides an unusual opportunity for a truly blind test of a sociobiological theory and should be a high priority for future research. If the theory is correct, then social insects will prove to be extraordinary not only for having evolved a higher level of colonial organization but also for having regressed to a lower level. The forging of the superorganism leaves only a few arenas in which individuals can assert their own interests, and it is in exactly these arenas that genomic imprinting undermines the individual from below. As a consequence, coherent individual interests may have been nearly eliminated. The many individual bodies that make up a colony are still there, but their self identity may be erased, leaving strange hybrid puppets animated from above by the strings of a marionette master but also from beneath by the rods of a pair of shadow puppeteers.

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