The police state


F. RATNIEKS

On the surface, beehives and ant nests seem to be model societies, with each individual striving for the common good. But maintaining this social order sometimes calls for brutal tactics. John Whitfield reports.

Murder, torture and imprisonment — these are the standard tools of repressive regimes. But if you imagine that human societies have a monopoly on such tactics, think again. Social insects perfected the police state long before people got in on the act.

The workers in bee, ant and wasp colonies forgo their own reproduction to raise the brood of their queen. Such is a worker honeybee's devotion to the collective, she will eviscerate herself by stinging any animal rash enough to attack the hive — a selflessness that has long fascinated naturalists.

We now know that workers receive their evolutionary payoff through their relatedness to the monarch. As the queen's daughters, they share many genes with her other offspring. By caring for the regal brood, they ensure their own genetic inheritance.

But in any society, it is possible to prosper by breaking the rules. Worker honeybees do occasionally lay their own eggs. As well as being against the queen's interests, this puts them at odds with the rest of the workforce. And in the late 1980s, evolutionary ecologist Francis Ratnieks, now at the University of Sheffield, UK, showed that honeybee workers act as a 'police force' that cracks down on miscreants, eating their eggs[1]. "Worker policing is a mechanism by which a society resolves its conflicts," says Ratnieks. "I think it's the best example of conflict resolution in nature."

Policing by egg-eating is common to all species of *Apis*, not just the familiar domestic honeybee, *A. mellifera*[2]. And bees are not alone — the phenomenon has recently been observed in some species of wasp[3] and in a group of ants[4]. "It may be very widespread," says Ratnieks.

But sometimes policing breaks down. Beehives occasionally dissolve into anarchy, as workers begin to reproduce *en masse*[5]. And a parasitic subspecies of honeybee is wreaking havoc in South Africa, destroying colonies by evading their police[6]. Evolutionary biologists hope that studying such face-offs between authoritarianism and anarchy will provide a deeper understanding of the balance between cooperation and selfishness


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A honeybee kills an a renegade worker's egg, left.

at many levels, from genes within the genome to individuals in human societies.

Sociality has evolved about a dozen times in the Hymenoptera — bees, wasps and ants. This is probably linked to their unusual method of sex determination, called haplodiploidy. In the Hymenoptera, sexual reproduction always produces female offspring, which are diploid — they have two sets of chromosomes, just like humans of both sexes. Male hymenopterans, however, develop from unfertilized eggs, and carry only one set of chromosomes. These 'haploid' males produce sperm that are genetically identical. This is different from diploid animals, which shuffle maternal and paternal chromosomes into their haploid sperm or eggs, giving infinite genetic possibilities.

Family ties

In human families, brothers and sisters each share half of their genes by common descent — their coefficient of relatedness (r), to use the technical term, is 0.5. The same is true for parents and offspring. For half-brothers or half-sisters, r is 0.25.

But haplodiploidy creates some bizarre family dynamics (see diagram, opposite). A mother's relatedness to her son is 0.5, but consider the same relationship from his perspective and r rises to 1.0. Sister–brother relationships are also unequal: from the sister's viewpoint, r is 0.25; from the brother's, it is 0.5. Mothers and daughters have a relatedness of 0.5, whichever way you look at it, and r for two sisters is always 0.75.

These final two figures are key, because they mean that a female can pursue her genetic interests more effectively by raising her mother's daughters rather than her own. This helps to explain why most females in social Hymenoptera do not reproduce. If the


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Police supervisor: Francis Ratnieks was the first to describe honeybees' disciplinary tactics.

An egg-laying worker bee (marked) is ignored...

...but this ponerine ant is assaulted by fellow workers as a punishment for attempting to reproduce.

B. HÖLLDOBLER

queen is mother to the entire female workforce, they have little to gain by producing their own daughters.

In many species, workers are physically incapable of mating. And in honeybees, the monarchs exploit their subjects by mating with up to 20 males; workers are thus tending to young that are mostly half, not full, sisters, with a relatedness of 0.375 rather than 0.75.

Worker honeybees cannot rebel by mating, but they can lay unfertilized eggs that will develop into sons, with a relatedness of 0.5. But *r* once again explains why other workers destroy sneakily laid eggs. To most of the workforce, another worker's son is a half-nephew, with a relatedness of just 0.125, so the majority gain if workers' eggs are culled and everyone concentrates on raising the queen's brood. The result, as Ratnieks has found, is a police force so pervasive that it rivals the former East Germany's infamous Stasi.

God save the queen

At the top of the security apparatus sits the queen, producing pheromones that instruct the workers to carry on with the usual business of repression. Most loyally shut down their ovaries and keep watch for any subversives. In this way, the success of worker policing is conspicuous by the rarity of transgressors. Only about 3 of the 30,000 or so worker honeybees in a typical hive have functioning ovaries, showing the inequality of the struggle between a lone selfish worker and the rest of her caste. Although these rogue females can lay about 7% of a colony's male eggs, effective policing means that only 1 in 1,000 males has a worker for a mother[7].

Indeed, workers' eggs usually get eaten within hours of being laid[1], betrayed by their lack of a chemical badge unique to the queen's eggs[8]. Honeybee workers also seem to detect when their colleagues are about to break the rules, becoming aggressive to workers with active ovaries[9]. But as with human dictatorships, the death of the leader can trigger major societal changes. When the queen dies, and her pheromones no longer pervade the hive, the workers hurl themselves into a frenzy of egg-laying[10].

Honeybees are the most advanced insect police state so far discovered. Wasp societies are smaller and simpler, but give another elegant example of animal behaviour matching evolutionary theory. Again, it all comes down to *r*. In some species of vespine wasp, the queen mates with just one male, whereas in others she mates repeatedly. Where queens are monogamous, and all workers are therefore full sisters, the relatedness between a worker and a fellow worker's son rises to 0.375, compared with 0.125 for species in which the queen mates several times. In both cases, workers are related to the queen's sons by an *r* of 0.25.

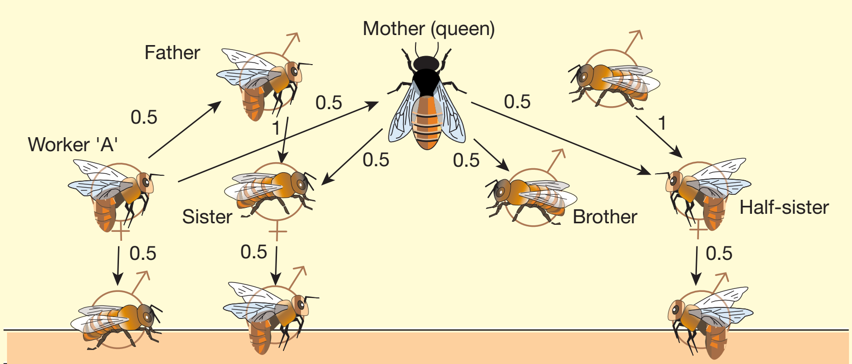
So workers should tolerate one another's egg-laying if their queen mates just once — because 0.375 is greater than 0.25 — but clamp down on renegade egg-layers if the queen is more promiscuous. Sure enough, this is what Ratnieks and his Sheffield colleague Kevin Foster found when they compared different wasp species[3]. They even saw policing varying within species: in the saxon wasp (*Dolichovespula saxonica*), queens may mate once or several times. Policing only occurs in colonies with promiscuous queens[11].

The fascist regime

In some ponerine ants, both social structure and policing are much less sophisticated. Living in colonies of 100 or fewer individuals in tropical forests, these ants have no rigid divide between queen and workers. Instead, all females have the potential to reproduce sexually. But only one or a few do, because small colonies cannot support many breeders.

Breeding females are called gamergates, and head a pecking order that has older workers at the bottom and younger workers — wannabe gamergates — in the middle. This hierarchy is enforced by both egg-eating and more brutal policing methods. If a young worker attempts to reproduce, she is spreadeagled by her fellows and kept immobilized for hours or even days. At the end of her sentence, the best she can hope for is a reduction in rank and loss of reproductive capability. Often she is mutilated or killed[4].

But ponerine gamergates do not enforce the same iron control over their security appa-



	Sister	Half-sister	Own son	Son of full sister	Queen's son (brother)	Son of half-sister
Worker 'A'	0.75	0.375	0.5	0.375	0.25	0.125

Numbers game: to determine the degree of relatedness between a worker and her nest-mates, follow the arrows, multiplying the values on each route and adding the products.

ratus as honeybee queens. From time to time, the ant police force stages a coup, deserting a failing ruler for a young pretender. "When the current reproductive is declining in fertility, workers can change allegiance," says Christian Peeters of the Pierre and Marie Curie University in Paris, who studies ponerine ants.

Even in honeybees, workers can overthrow their monarch's reproductive monopoly by activating their ovaries and tolerating one another's eggs[5]. But such anarchic hives are very rare. Ben Oldroyd of the University of Sydney, who studies the phenomenon, has sought out examples by placing adverts in beekeeping magazines. "We've had two reports in seven years of advertising," he says.

Oldroyd suspects that this is because honeybee anarchy requires a mutational double whammy: worker bees must ignore the pheromones that suppress their ovaries, and must also produce eggs that evade policing, probably by counterfeiting the queen's chemical signal. Oldroyd's team has shown that ovary activation and egg-faking are under separate genetic control: they have managed to breed both egg-laying workers whose eggs are detected and destroyed by their fellows, and workers that do not lay eggs, but do not destroy workers' eggs transplanted into the colony[12].

Breeding for anarchy

Naturally anarchic hives contain a few dozen laying workers, and seem to function well. But by selective breeding, Oldroyd and his colleagues have got the egg-layers up to about 40% of the workforce. In these hives, breeding workers neglect their chores and the hives become decadent to the point of collapse[2]. "They can barely feed themselves, and they do weird things like trying to raise queens out of male larvae," Oldroyd says.

These selectively bred anarchist hives have some other odd features. Normal workers transplanted into them may start laying[13], which suggests that the queen's pheromones are weaker than normal. Most strangely, taking the queen out of an anarchic colony — which triggers worker egg-laying in normal hives — causes anarchic workers' eggs to lose their deceptive properties. They are eaten if transplanted into a normal hive, says Oldroyd.

Oldroyd and his team are trying to identify the genes that influence anarchic behaviour.

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Point of order: Ben Oldroyd has bred anarchic bee colonies, but this is very rare in nature.

If they can find them, it will provide a long-awaited mechanism for theories about animal conflict and cooperation. "Anarchy genes are genes for selfishness, and anti-anarchy genes are genes for altruism," says Oldroyd.

A honeybee hive's policing can also be subverted from the outside. In January this year[6], Ratnieks's team described studies of a parasitic form of the Cape honeybee (*A. m. capensis*), a freeloader that over the past decade has cut a swathe through hives of the African honeybee (*A. m. scutellata*) in northern South Africa. The parasitic Cape workers are like Oldroyd's anarchists in that they do little work. But instead of laying haploid male eggs, they produce diploid female eggs that are genetic copies of themselves[14].

Ratnieks and his colleagues have shown that the African workers cannot distinguish these eggs from those of their own queen — presumably because the Cape bees use some sort of chemical counterfeit. As a result, the invaders' numbers grow so quickly that the colony is destroyed within months. The Cape bees then move on to another hive.

Formerly confined to the southernmost part of South Africa, Cape honeybees were probably spread to the hotter north of the country, which is favoured by *A. m. scutellata*, by South African beekeepers who move their hives around to catch the blooming seasons of different flowers. This nomadic beekeeping style is still aiding the parasite's spread.

The parasitic Cape bee now plagues an area of South Africa about 400 by 200 kilometres in size, stretching from Pretoria to the border with Mozambique. The parasite's ability to produce exact clones of itself, keeping its clique of selfish genes together, makes it a formidable fifth-columnist. "We spread the net as far as we could, and everything we've caught has been the offspring of a single worker," says Per Kryger of the University of Pretoria, who is monitoring the problem.

Bees not for keeps

"Many beekeepers are losing 100% of their colonies each year," Kryger says. "The only reason they're still in business is that they collect swarms from the wild." Kryger estimates that 50,000–100,000 wild *A. m. scutellata* swarms per year are lost to domestication — and subsequent parasitism. If the trend continues, he says, the local survival of the African honeybee will be threatened.

Kryger is trying to work out whether the parasitic form is also common in the Cape bee's home range. He suspects that *A. m. capensis* may have evolved countermeasures to deal with its seditious element. Exactly what these might be remains unclear — normal Cape honeybees show policing behaviour, but this is not especially pronounced[15].

Studies of such conflicts may also yield insights into other aspects of biology, and even the social sciences. Laurence Hurst, an evolutionary geneticist at the University of Bath, UK, draws parallels between worker policing and the mechanisms that genomes have evolved to prevent individual genes from inserting themselves into a disproportionate number of sperm or eggs.

"Worker policing is a nice case history for examining the conflicts present in any social structure," Hurst says. He believes that it may be possible to derive theoretical models to capture accurately the dynamics of conflict in everything from genomes, through social insects, to human society. "There are important differences between different systems, but there are also abstract features that unite them. It isn't just a metaphor," he says. ■

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Insect invasion: an African honeybee (right) unwittingly feeds one of an army of parasitic Cape bees.