Queen Control, Worker Policing, Anarchy and Law in Honeybee Society (*Apis Mellifera)*

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– Prelude–

Nascent theory in science is often based more in cultural fiction than scientific fact. Individuals do not create their worldviews by pure, objective scientific reasoning and observation. Most of what we know is taught to us by other people (i.e., by transmission of collective knowledge – that is, by culture). Science often proceeds by first articulating the collective belief of a culture (e.g. "the world is flat") and then by replacing this belief with another theory ("the world is round") when appropriate supporting evidence is brought to hand.

Anybody with culture (i.e. everybody!) is bound to make these kinds of 'mistakes' (of cultural 'fiction' over scientific 'fact'). It just goes to show: we learn first from others, then the universe we live in (i.e., culture first, science later). This is, of course, why we have science. This is why, during the Renaissance, Western people began overturning the collective knowledge of their institutions (of, say, Church and state). At least since the Renaissance (and maybe before), the collective psyche of western culture has harboured a deep suspicion for the collective knowledge transmitted from 'the ancestors'. The scientific and industrial revolutions of the 16th and 17th centuries were spawned by this collective feeling – by the feeling that 'truth' was being obscured by culture; by the feeling that the ancestors were wrong; by the feeling that, despite this, the truth was 'out there' to be revealed (by proper observation of the behaviour of the universe).

A common (i.e. collective) belief pervading the modern (and modernising) world (or rather, the modern world*view* – i.e., the world in peoples' heads, not the physical world 'out there') is: someone (or some group of 'ones') needs to be in control of human society – i.e., we need rulers, leaders, governments and 'heads of state' – making and enforcing law, without whom, society would disintegrate into 'anarchy' (whose common dictionary definition is "absence of government; disorder, confusion"). In other words, for human society to exist, people need other people making laws, telling them how to live (i.e., spelling out and enforcing 'right' and 'wrong' behaviour). This is common, widely accepted knowledge among the people of our culture, but it is very much like saying "the universe needs scientists making laws telling matter how to behave".

We all know that gazelles don't need other gazelles making laws telling them how to behave (and gazelles don't live in anarchy). We also know that lions, wolves, sticklebacks, polar bears and chimpanzees don't need other lions, wolves, sticklebacks, polar bears and chimpanzees making laws telling them how to behave (and that lions, wolves, sticklebacks, polar bears and chimpanzees don't live in anarchy). Yet, for some reason, we accept (without question) that people do.

Of this, our collective knowledge says: people need other people making laws, telling them how to live, because human society is more 'advanced', more complex and therefore more 'perfect/refined' than simpler (and therefore less perfect/refined) animal societies. When the 'early' sociobiologists (like E.O. Wilson, 1971) began to investigate other so-called 'advanced' and complex animal societies, like those of the eusocial hymenoptera, they theorised that the existence of a specialist 'queen' who mothered all (or at least, most) of the society's offspring, meant that she controlled (i.e. ruled – made and enforced law for) the colony (see Keller and Nonacs 1993). As I have already said, nascent scientific theory often starts with the collective (cultural) belief of a people (or society) only to replace this belief with a theory that makes better sense of the existing evidence. Something like this has happened (or rather, *is* happening) to our understanding of 'queen control' theory in honeybee (*Apis mellifera)* society.

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– Introduction –

Keller and Nonacs (1993:787) define queen control as:

> …workers or subordinate queens being manipulated by a dominant queen into pursuing actions that are contrary to their inclusive fitness (or conversely, workers can only do what is best for themselves when queens are dead or absent).

In small hymenopteran societies queen control was proposed to occur by physical intimidation leading to the formation of dominance hierarchies between queens and their subordinate workers. In larger hymenopteran societies (*A. mellifera* colonies number up to 60,000 individuals – Barron, Oldroyd and Ratnieks 2001), queen control by physical intimidation was thought unlikely. Instead, coercion of workers was proposed to occur by 'pheromonal queen control' whereby chemical substances exuded by queens force workers to behave in ways that increase queen fitness (Keller and Nonacs 1993, Wilson 1971).

Like every discarded scientific theory, queen control theory could predict some, but not all of the observed phenomena. For example, in some small hymenopteran societies (sweat bees, paper wasps and bumblebees, for example) indeed, queens do physically force workers from oviposition (Ratnieks 1988). And in some large societies, like *A. mellifera*, workers refrain (almost entirely) from reproducing. As well, evidence suggests that queens do produce pheromones that suppress ovary development in workers (although it seems likely that both brood and queen produce these pheromones – Barron and Oldroyd 2001; Barron, Oldroyd and Ratnieks 2001; Oldroyd, Wossler and Ratnieks 2001; Ratnieks 1988). But, although 'queen control' may appear to account for, at least, some of these phenomena, there is much more that it cannot explain. Why, for example, in some queenright hymenopteran societies, do queens 'allow' workers to contribute to the brood (Ratnieks 1988)? Why, in others, do workers lay eggs that are 'policed' by other workers (i.e. aggressively attacked and their eggs eaten – Ratnieks 1988)? Why, in some worker-policed societies, do 'anarchistic' traits occasionally appear where workers 'get away' with laying eggs and avoid worker policing (Barron, Oldroyd & Ratnieks 2001; Oldroyd, Halling & Rinderer 1999; Oldroyd & Osborne 1999; Oldroyd & Ratnieks 2000)? The answer is, of course, that queens are not in control of the societies to which they belong. If anything is making the law, it is natural selection.

– Paranoid People and Controlling Queens –

Queenright hymenopteran society is not as 'controlled', 'perfect' nor 'refined' as queen control theory predicts. This is because evolution by natural selection does not work to produce controlled, refined or perfect systems. Natural selection selects for the first workable (or, evolutionarily stable) system and then stops there. Organisms do not 'aim' to evolve. They aim to produce exact copies of themselves (or, at least, of their genes – Dawkins 1989). Life does not aim to be 'perfect'. Individuals aim to reproduce (their own genes, regardless of how prefect or imperfect they are). For this reason, queen control theory has been (largely) eclipsed by evolutionary theory (although much of the language spawned by it – 'social hierarchy', 'queen control', 'anarchy', 'policing' – remains in the literature, like vestigial organs).

First, 'queen control' is not an evolutionarily stable strategy (or ESS – see Dawkins 1989) because, in the absence of personal fitness gains, natural selection would favour the spread (or invasion) of any gene conferring immunity (or tolerance) to controlling pheromones (Keller and Nonacs 1993). Second, if queens truly were "in control", there should be no need for "worker policing" since no workers should be fertile (Keller and Nonacs 1993). Third, worker reproduction is well known in other queenright societies, in particular, those species whose queens are monandrous (i.e., mate only with a single male) tend to have higher rates of worker reproduction (Ratnieks 1988). Cape honeybee (*Apis mellifera capensis)* queens are polyandrous (i.e. mate with several males – like *A. mellifera*) and show worker reproduction *and* reduced worker policing (compared to *A. mellifera*). *A. m. capensis* workers lay diploid (i.e., female) eggs (produced by thelytoky, not fertilization) and have strongly reduced worker policing (Moritz, Kryger and Allsopp 1999). But, regardless of the criticisms and inconsistencies, no theory is replaced by being debunked. A theory is replaced when another theory comes along that better explains the observed phenomena. Queen control theory has been eclipsed by a branch of evolutionary thought called 'inclusive fitness theory' that explains what queen control theory cannot.

Along with a deep suspicion for the received wisdom of our culture, westerners have, since before Carl Marx's time, been deeply suspicious of their social leadership, the ruling minority – or as Marx called them, the 'owners of the factors of production' or the 'bourgeoisie' – who profit at the expense/exploitation of the labour of the non-ruling majority – Marx's 'working class' or 'proletariat' (Cuff *et al.* 1998). As with other nascent theory, the 'early' sociobiologists initially sought to prove common wisdom – that large, complex (or 'advanced') animal societies evolve in analogy to 'advanced' human society. That is, natural selection favours the evolution of a specialized class (or caste) of individuals ('Kings', 'Queens', 'governments', etc.) who endeavour to control the rest of society ('worker' classes/castes); benefiting at the expense of the majority; achieving this end via physical force (by 'policing' laws invented by them – "thou shalt not reproduce") and/or via powerful subliminal, coercive (yet irresistible) messages (i.e., 'pheromone control'… 'television'!). Although there is good reason to believe that these tensions exist (and therefore evolved) in so-called 'advanced' human societies (i.e., that the sentiments of, say, Carl Marx and George Orwell are well justified), there is little to suggest that these tensions exist in hymenopteran society. According to inclusive fitness theory, the

tensions in honeybee society are of an entirely different flavour. I suggest, then, that queen control theory is the product of an engrained (Marxian-Orwellian) paranoia that exists within the collective psyche of 'advanced' human society. That is, it is a projection of our so-called 'advanced' culture (as are most nascent scientific theories) upon the universe, and specifically, upon hymenopteran society.

– Inclusive Fitness Theory –

In terms of inclusive fitness theory[1] relatedness is the locus around which so-called 'altruistic' (to sacrifice personal benefit for the good others – Gleitman 1995) behaviours evolve (Dawkins 1989, Hamilton 1964a and 1964b). According to the theory, the evolution of social behaviours that increase the reproductive fitness of other individuals at the expense of one's own has nothing to do with altruism (being "nice" or "good") and everything to do with reproduction (specifically, making copies of, and passing on, one's own genetic code). Inclusive fitness means making an assessment of fitness that includes those genes an individual shares with their relatives, or kin. By helping a close relative to reproduce, individuals ensure the reproduction of the genes they share – increasing their 'inclusive fitness'. There comes a point where, if one helps enough close relatives to reproduce, the reproduction of one's own genome is almost entirely ensured. Helping behaviours are proposed to evolve by 'kin selection'. If you have a gene that encodes for you to help your parents to raise their children, there is, on average, a 50% likelihood that your parents child will carry that gene. In this way, genes for kin helping kin raise children can replicate and spread through populations – by kin selection (Dawkins 1989, Hamiltom 1964a and 1964b).

In honeybee society, workers share 50% of their genome with the queen (their mother). And because honeybees are haplodiploid (males haploid and females diploid – Hamilton 1964b), full-sisters share, on average, 75% of their genome. From these figures of genetic relatedness alone it is apparent why workers should help queens raise daughters (their sisters, with whom they share 75% of their genome, if they are full-sisters) rather than help sisters raise daughters (workers share, on average, only 37.5% of their genome with full-sisters' daughters). Even if queens are polyandrous, half-sisters still share more of their genome (on average, 25%) with one another than with half sisters' daughters (on average, 12.5%). In fact, workers share, on average, more of their genome with their sisters (75%) than with their own daughters (with whom they share 50% of their genome). Explaining, in terms of inclusive fitness theory, why workers should evolve behaviours for helping mothers produce daughters is relatively simple, but not nearly so simple for explaining why workers should help mothers produce sons.

Workers share, on average, 25% of their genome with their brothers. No matter how many fathers the hive has (i.e., how many males the queen mated with on her 'mating flight') workers always share 25% of their genome with their brothers. This is because males are produced by arrhenotoky (i.e., the development of an unfertilised egg). On the other hand, workers share, on average, 37.5% of their genome with their full-sisters' sons. Furthermore, workers share 50% of their genome with their own sons

[1] Otherwise known as 'kin selection' theory after the work of W.D. Hamilton.

(see Figure 1). Inclusive fitness theory would suggest, then, that full-sisters evolve behaviours to help (in order of priority): (1) themselves raise sons; (2) random full-sisters raise sons; and (3) queens raise sons (Ratnieks 1988). Indeed (as I have already said) we find, in hymenopteran societies where queens are monandrous and where, hence, all workers are full sisters (e.g. stingless bees, bumblebees – Peters *et al.* 1999, Ratinieks 1988) the tension between individual reproduction and queen reproduction is resolved in favour of a high frequency of male production by workers. Honeybee queens, however, are not monandrous. On mating flights honeybee queens mate with many males (are polyandrous) keeping each one's sperm to fertilise future eggs, producing the colony's future workers. From here, things get a bit more complicated.

Because honeybee queens mate with many males, the colony becomes genetically divided into a series of 'subfamilies' whose number is the same as the number of queen's mates, *n*. Each of these subfamilies is composed of full-sisters whose relatedness is 0.75 (i.e., sharing, on average, 75% of their genome). Between subfamilies, the relatedness of half-sisters is, as I have said, 0.25. As the queen's mating frequency, *n*, increases the average relatedness of sisters to a random sister's son decreases from 0.375 to 0.125 (see Figure 1). This means that if the queen was mated to more than 2 males, the average relatedness of workers to a (random) sister's son (<0.25) is less than the average relatedness of workers to queen's sons (always 0.25). No matter how many times queens mate, workers are still related to their own sons by a factor of 0.5. Inclusive fitness theory would suggest, then, that honeybee workers evolve behaviours to help (in order of priority): (1) themselves raise sons; (2) queens raise sons; and (3) random sisters raise sons (Ratnieks 1988). Our prediction, then, is that the inherent tension between individual workers (selves), queens (mothers) and other workers (sisters) be expressed in honeybee social life (i.e. the 'law of honeybees', if you like).

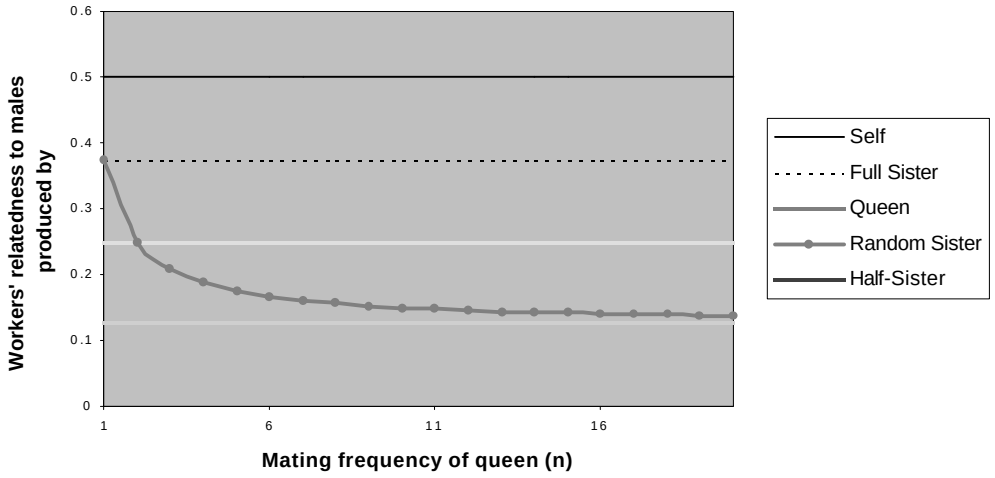

Figure 1: The relatedness of colony workers to males produced by: themselves; full sisters; queens; random sisters; and half sisters, for colonies with different mating frequencies of queens, *n*. [Adapted from Ratnieks 1988:218]

From what we know of honeybee behaviour (by careful observation) we can say the 'law of honeybee workers' includes the following observed behaviours: "Help queens

raise daughters"; "If you can, produce sons"; "If you can't produce sons, help raise queens' sons"; "When queenright, attack fertile sisters (esp. in oviposition) and eat sisters eggs" (Barron, Oldroyd and Ratnieks 2001; Peters *et al.* 1999; Ratnieks 1988; Ratnieks and Visscher 1989). This isn't because these behaviours are "right" or "good" or enforced by their 'leader' (the queen). This is because the genes for these behaviours, and the genes encoding for the production of influential chemicals (say, pheromones), evolved by natural selection and are evolutionarily stable (i.e., cannot be bettered nor subverted by another strategy). Evolution doesn't select for "right" or "good" or "moral" or "perfect" behaviours. Natural selection simply sorts the workable (i.e., reproducible) from the unworkable (i.e., dead or dying). Inclusive fitness theory can be used to account for the workability (not the perfectibility) of honeybee law.

Because honeybee workers share more of their genetic code with their own sons than with their queen's sons and (on average) their sisters sons, inclusive fitness theory predicts that workers attempt to lay male eggs, despite whatever the cost to colony efficiency. But, since workers share less of their genome with random egg-laying sisters than with their queen, workers are likely to evolve behaviours that favour the rearing of queen's sons over random sisters' sons. It is testimony to the frugality of "nature's economy" (see Worster 1985) that sisters' eggs are eaten and not simply discarded (again, not because nature is 'noble' or 'good', but because this behaviour contributes more to the fitness of individuals than any other behaviour would). The outcome is that, despite contributing a significant number of male eggs to the colony (about 7%), only about 0.1% of a colony's males are workers' sons (Barron, Oldroyd and Ratnieks 2001). The exceptions are colonies termed 'anarchic' for their high representation of workers sons (Barron and Oldroyd 2001; Barron, Oldroyd and Ratnieks 2001; Oldroyd, Halling and Rinderer 1999; Oldroyd and Osborne 1999; Oldroyd and Ratnieks 2000; Oldroyd, Wossler and Ratnieks 2001). But, as we shall see, this unusual behaviour has nothing to do with disregarding the law, but everything to do with following the law.

– Bee Against the Law and Bee Dead –

Although it is difficult to say, given the current evidence, Barron, Oldroyd and Ratnieks (2001) estimate that one out of every few hundred, or maybe every few thousand, honeybee hives display a partial breakdown of worker policing and of the pheromonal systems that maintain normal (or 'wild-type') reproduction of males. In natural anarchistic colonies (i.e., those that have not been artificially selected – see Oldroyd and Osborne 1999) about 1% of workers have fully developed ovaries (cf. 0.01% in wild-type colonies); the majority of workers sons are from a single patriline (or subfamily); worker policing of laying workers and their eggs is significantly reduced; hence the representation of workers' sons in the brood is significantly higher (Barron, Oldroyd and Ratnieks 2001).

In his seminal 1988 paper on inclusive fitness theory and worker policing, Francis Ratnieks suggested that queens might evolve a queen-specific egg-marking pheromone only if workers with the ability to mimic this pheromone could, themselves, be detected and stopped. Further studies revealed the existence of such a queen-specific egg-marking pheromone excreted, it seems, from the Dufour gland of

queens (Barron, Oldroyd and Ratnieks 2001; Keller and Nonacs 1993; Ratnieks and Visscher 1989). What Ratnieks failed to take into account (surprisingly) is that both queens and workers mutually benefit from the presence of these chemicals in the reproduction and maintenance of the colony. Oldroyd and Osborne (1999) report that in colonies where genes for 'anarchic' behaviour are artificially spread (by the instrumental insemination of daughter queens in an anarchic colony with sperm from their nephews – the sons of their anarchistic sister workers) 5 to 10% of workers have active ovaries. Soon, workers' larvae become so common that up to 80% of the brood is male (Barron, Oldroyd and Ratnieks 2001). Carry this scenario a little further and it is easy to see why both queens and workers benefit from the presence of queen-specific egg-marking pheromones and why genes for 'cheating' cannot spread.

Counterfeit pheromones do not need to be detected and stopped, as Ratnieks (1988) proposed. Colonies where the behaviour is widespread simply disappear – i.e., are eliminated by natural selection. But although the widespread employment of this strategy is not evolutionarily stable, occasional employment is, and this is what appears to be happening in so-called 'anarchistic' colonies.

The law of the honeybee worker is: "If you can, produce sons". Inclusive fitness theory therefore predicts that a gene for producing counterfeit egg-marking pheromones, allowing workers' eggs to go undetected and therefore unpoliced, might arise (Ratnieks 1988). However, as Oldroyd and Osborne (1999) aptly demonstrate, the spread of such a gene causes the colony (and therefore the gene) to die. But this only occurs if the gene spreads. In other words, natural selection should favour the persistence of an 'anarchic' gene that maintains itself at a low frequency of expression. As it turns out, expression of the anarchic trait appears to depend upon the coincidental expression of not one, but several loci (Barron, Oldroyd and Ratnieks 2001). The second generation, in Oldroyd and Osborne's (1999) experiment, gave rise to four classes of colonies, in terms of worker reproduction (see Table 1). It appears that the two traits of (a) 'ovary activation' and (b) 'ability to lay eggs that are not policed' segregate independently. The different possible combinations of expression of these two loci appear to produce the four classes of colony in Table 1. It appears, then, that the 'anarchic' trait is only expressed when workers of a single patriline have both (a) active ovaries and (b) the ability to lay eggs that are not policed (Barron, Oldroyd and Osborne 2001).

1. No ovary activation detected in any of the circa 100 workers per colony examined.
2. Ovary activation in the daughters of the anarchist males, but no detectable larval, pupal or adult male production by workers.
3. Ovary activation in workers from both anarchic and non-anarchic patrilines but no male production by either kind of worker.
4. Ovary activation and adult/pupal male production by worker daughters of anarchist males.

Table 1: The four classes of worker reproduction in the artificially selected anarchistic colonies of Oldroyd and Osborne (1999). Table reproduced directly from Barron, Oldroyd and Ratnieks (2001:205).

– Conclusion –

The existence of a so-called ‘anarchic’ trait in the occasional honeybee colony represents not the absence of law, but the presence. The underlying order (or logic) is exposed by inclusive fitness theory. Individuals seek to invest in offspring with whom they share the greatest proportion of their genome. In the case of honeybees, workers share more of their DNA with their own male offspring than with anyone else’s. However, if a large proportion of workers began to produce eggs that escaped policing, the entire colony (and therefore, every individual’s genome) is threatened. Natural selection does not select for the “best” outcome, just the first workable one. In the case of *A. mellifera,* natural selection mediates between the social tensions created by the genetic structure of the species to produce an outcome that is not ‘perfect’ (although perfection is, of course, in the eye of the beholder), but which enables genes to replicate. This includes, so it seems, a series of genes encoding for traits like the activation of workers’ ovaries and the production of egg-marking pheromones that mimic those produced by queens. Law is created through the interplay of genes attempting to reproduce themselves and natural selection preventing them. This is law, not anarchy.

– Epilogue –

For a theory with such capacity to explain the evolution of social behaviours, inclusive fitness theory has been incredibly slow to be applied to the study of animal behaviour (see Dawkins 1989:90, 325-329). Testimony to this fact is that, in 1988, Francis Ratnieks was the first (as far as I know) to apply the theory to the study of worker policing in eusocial hymenoptera. This is an incredibly long incubation period for an idea implicit in the writings of R.A. Fisher and other pioneers of neo-Darwinian thought in the 1930s (Dawkins 1989), made explicit by Hamilton in the 1960s. And in disciplines outside of evolutionary biology, inclusive fitness theory hardly ever gains a mention.

Any theory that threatens to eclipse a fervently held collective belief will be ignored for as long as it possibly can. Long before we start learning from the universe (i.e., through science) we are taught: the law of human society is invented by people (specifically, our leaders) and written in books. Although, as students of ethology, we know that the 'law of honeybees' (if we choose to call it this) is written in the behaviour of honeybees ("Help raise queens daughters", "When queenright, eat sisters eggs"), and nowhere else, we seem content to believe that the law of our species needs to be invented (lest people live in lawlessness, i.e., anarchy). Kin selection theory exposes the genetic logic behind the unwritten (i.e., evolved) laws of animal behaviour.

If a new idea comes along (e.g., "there is a genetic logic behind the social behaviour of honeybees that has nothing to do with 'queen control'") people are entitled to ask: how is this so? And if the answer provided by the new theory provides a better depth of explanation to the observed phenomena than the previous idea, people are entitled to discard the old belief (and hopefully they do). This is why the logic of kin selection has taken so long to be, and is still so rarely, applied. It provides a depth of explanation to animal behaviour that eclipses the simple "right"/"wrong" answers of written, moral law. Just as it exposes the genetic logic behind the unwritten laws of animal behaviour, it threatens to expose the unwritten logic behind human social behaviour (and hence, why written law fails, consistently, to predict human behaviour). People are afraid to wonder: Does *Homo sapiens*, like every other species, have law beyond that invented by their leaders? Does there exist a social structure to which this 'evolved law' is adapted? Could it be that, outside of the laws inverted by our leaders, lies not anarchy, but a workable human social order? People are (understandably) afraid to explore the logic of kin selection. It's as though they sense the magnitude of what the idea threatens to reveal, and at the same time, eclipse.

We (i.e., the people of modern culture) like to talk about control in animal societies because it makes a good bedtime story for the children of modern society, reinforcing the view that social creatures are (by nature) controlled by a single entity ('King', 'Queen' or 'government'), playing both upon our sense of enforced social order and upon our sense of oppression. But while these sentiments are understandable for a culture bent upon world domination and the seizing of ultimate power over life and death in the universe, this point of view cannot be extended to the evolution of animal society. Their primary concern is not to rule the world, but to make a living and reproduce their genome.

This simple ambition ensures that law is something they hold without contempt. 'Anarchic' honeybees are not trying to overthrow the law. They are living within the law. How could any behaviour evolve (by natural selection) outside of the law? To live outside of the law is to die (along with the behaviours encoded by your genes – "Bee against the law and bee dead"!). This is solemn warning for those who believe it their destiny to make the law. Our modern wisdom says: "People not only have to invent laws for other people, but also for the rest of life on earth." Of course I am referring here to 'artificial selection' (although nowadays it goes by other names, like 'genetic engineering'). Artificial selection means shaping life according to laws invented by people: "Grow bigger"; "Grow faster"; "Grow resistant to salt". Artificial selection is the mainstay of the modern economy and the prime-mover in the social evolution of so-called 'advanced' society. This, however, is another story (to be expounded in a thesis next year!).

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