The veil of ignorance can favour biological cooperation

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Lack of information is a constraint but ignorance can sometimes assist the evolution of cooperation by constraining selfishness. We discuss examples involving both ignorance of role or pay-off and ignorance of relatedness. Ignorance can favour cooperative traits like grouping and warning coloration and reduce conflicts from meiotic drive, imprinting, greenbeards and various forms of nepotism.

1. Introduction

Ignorance never settles a question
Benjamin Disraeli, in a speech in the House of Commons

Ignorance is strength
George Orwell, in 1984

Of the two quotes above, the one by Disraeli surely comes closer to the mark. It is generally bad to be ignorant. Indeed, Orwell’s quote was satirical, though 1984 did illustrate that individual ignorance could strengthen groups. The philosopher John Rawls [1], following John Harsanyi [2], put ignorance to a related but nobler purpose. They suggested deploying a veil of ignorance to decide what behaviours are just. The essence of the argument is that decisions on apportionment of goods should be separated from knowledge of personal gain, as when the cake cutter does not get first choice of a piece.

Non-human organisms do not make prescriptive moral judgments. However, there is a biological analogy, not for how organisms should behave, but for how they do behave [3–11]. When the state of an actor affects its fitness, but the actor is ignorant of its state, then selection acts on the average across all states, which corresponds closely to Harsanyi’s argument [5].

Ignorance is typically bad—it is better for a bee to know which flowers have the most nectar rather than to randomly sample flowers (unless knowledge is too costly). Ignorance is similar to three other evolutionary constraints that, when they constrain selfishness, can favour group function (table 1). First, low genetic variation is a powerful constraint on evolution, but relatively low genetic variation within groups (high relatedness) aids kin-selected adaptations [12,13]. Second, detrimental pleiotropic effects impede evolution, but can make cheating harder when cooperation is pleiotropic [14]. Finally, lack of power can benefit cooperation when the power of individuals to be selfish is reduced [8,15].

Hamilton’s inclusive fitness theory [12] shows that there are two components of fitness gain and therefore two arenas for ignorance: personal pay-offs and relatedness. Figure 1 illustrates some of the examples of both. We introduce both types with the example of meiosis.

2. Meiosis

Ignorance of pay-offs may be important in female meiosis [4]. Only one of the two alleles gets into the egg, so the potential twofold advantage of
preferentially entering the egg would favour this selfish trait even if it is associated with strong organizational disadvantages (either direct effects like aneuploidy when both chromosomes go to the egg [4] or indirect pleiotropic effects). Summed disadvantages across multiple loci could be disastrous. Mothers may therefore evolve to obscure information about which haploid cell becomes the egg versus which cells fail to get to the next generation [9]. There are few direct data on this, but a suggestive example comes from an exception to the usual rule of fair meiosis. Knob chromosomes in maize have extra spindle attachment sites [16]. This speeds their movement and increases their probability of being in one of two terminal cells of the linear tetrad, one of which will be the egg. The fact that they seek out the two ends of the tetrad suggests that they cannot tell which end will be the egg.

Ignorance of pay-offs has been invoked for the fairness of meiosis in both females and males; when each allele has a 50% chance of transmission to any given progeny, it can work only for the benefit of the organism [5]. But we believe that 50% fairness is less essential than the fixity of any transmission rule that suppresses within-individual competition [8]. For example, if nuclear genes absolutely control the sex ratio, mitochondrial genes that are transmitted only through daughters cannot harm the individual [16].

The fairness of meiosis also depends on ignorance of relatedness. Obtaining information about relatedness is difficult for a single gene, but two tightly linked mutations suffice if one encodes a diffusible poison and the other an antidote [9]. Tightly linked poison–antidote gene pairs underlie male meiotic drive loci [16]. The allele at the antidote locus is the relatedness cue for the poison allele; killing those who lack the antidote kills those who lack the poison. Recombination breaks up the poison–antidote pairings and effectively throws a veil of ignorance over information about relatedness, hampering the evolution of meiotic drive [9,17].

### Table 1. Evolutionary constraints that impede evolution, but can assist in the evolution of cooperation by impeding within-group selection.

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<th>impedes selfishness (favours cooperation)</th>
<th>impedes cooperation (favours selfishness)</th>
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<td>low genetic variation within groups</td>
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<td>pleiotropy of within-group fitness traits</td>
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<td>lack of power to affect within-group fitness</td>
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<td>ignorance of within-group fitness options</td>
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3. Ignorance of pay-offs

For many grouping behaviours, there are costs that only some individuals pay, but ignorance of who will pay means groups form based on the averages.

In many ants, colonies begin with small groups of unrelated queens [18]. They coexist peacefully, using their body reserves to rear the first cohort of workers, but then all but one queen is killed. The cooperative efforts of dead queens have been entirely for the success of a non-relative. Any queen who knew that it would lose would take its chances, however dismal, on nesting alone. However, under a veil of ignorance about its future state, each joins and invests according to the average pay-off of winning and losing.

The social amoeba Dictyostelium discoideum forms groups to build fruiting bodies in which 20% of cells die to form the stalk. Competing genotypes gain by avoiding becoming stalk. Becoming a stalk cell is correlated with nutrition, stage of the cell cycle and timing of entering the social process, but at the time of joining cells may be ignorant of their status relative to other cells [3].

A colourful distasteful caterpillar may die by attracting a naive predator, but teaches the predator to avoid the more memorable coloured caterpillars [19]. An individual who knew in advance that she would be in the teacher role would best opt for less conspicuous colours, except in cases where the teaching would specifically benefit kin. But as she cannot know, selection favours bright coloration with its higher average pay-off.

4. Ignorance of relatedness

Meiotic drive genes fit the definition of greenbeards; alleles that act based on their recognition of copies in others [20]. The lack-of-recombination requirement also applies to other greenbeards, perhaps accounting for their rarity. The gp-9 queen-killing greenbeard in fire ants occurs on a non-recombinant region. For the csaA greenbead gene in D. discoideum has little or no recombination because its greenbeard traits result from the cell adhesion its protein causes. Bacteriocins that harm other bacterial genotypes are common, but are the exception that proves the rule because they occur in bacteria that recombine rarely.

Ignorance of pedigree relatedness (as opposed to single-gene greenbeard identity) can also be important. We assume a veil of ignorance when we calculate relatedness as an average over the individual’s two alleles. Genes from the mother and father (matrigenes and patrigenes—[11]) are differently related to certain kin. An offspring’s matrigenes are related to maternal half-sibs, while its patrigenes are unrelated. They should therefore favour different behaviour to half-sibs, but cannot express this conflict under a veil of ignorance about parental origin. Most genes may indeed be ignorant of parental origin, but the veil can be lifted by genomic imprinting, in which parents differentially methylate genes passed on through sperm and eggs. Considerable evidence suggests that imprinting leads to conflict between matrigenes and patrigenes in an individual [21].

Other veils hide relatedness among individuals. A colony of social insects may include different classes of relatives, for example different patriline owing to multiple mating by the queen. Individuals could identify members of their own patriline if they used their own phenotype as a learning template and assessed similarity to possible beneficiaries, but they appear not to do so [11,22]. This is very puzzling because many social insects use colony mates as learning templates for phenotype matching, but not their own phenotype, so they cannot discriminate within colonies [11]. Likewise, though male birds will avoid rearing the broods of another male, as expected, they seem not to preferentially care for their own offspring in a mixed brood [22].

There can also be veils over non-genetic cues of relatedness. Worker–queen sex ratio conflicts may be mitigated when workers cannot identify brothers that they might prefer to eliminate [23]. Similarly, Hymenopteran workers should prefer to rear their own sons over the queen’s sons, but may be prevented from replacing a queen egg that might be either an undesirable brother or a desirable sister [24].

More extreme cases of relatedness ignorance in social insects include unicoloniality, slavery and social parasites, which all involve workers rearing unrelated young. Similar issues arise in parasitic birds and their hosts, which have evolved to balance discrimination against the intruder’s eggs with inadvertent removal of their own eggs.

### 5. When is ignorance strength?

Although we suggest that a veil of ignorance can paradoxically be helpful for group function, it is not always so.

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#### Figure 1. Selected outcomes with and without a veil of ignorance over (a) pay-offs and (b) relatedness. Drawn by Susanne DiSalvo, copyright CC3.0.
Ignorance about options that are good for the group is not helpful (table 1). It is impossible to reward, punish or ostracize without information about who defects. For example, social insect workers cannot police the egg-laying of other workers unless they can distinguish worker eggs from queen eggs. More generally, beyond the enforcement of cooperation, information is what allows much cooperation to occur. For example, the division of labour and coordination of activities in a social insect colony rests on reliable information.

6. Selection for ignorance

Ignorance may sometimes be an unselected constraint that fortuitously enhances cooperation. A warningly coloured insect presumably cannot know whether it will be eaten or protected. Without parental imprinting, a gene cannot know whether it is a matrigene or a patrigene. In other cases, ignorance results from a trait, for instance recombination, that may have been selected for other reasons.

The closest parallel to Rawlsian justice is when a party evolves to impose ignorance on everyone, including itself. The lack of a self-matching mechanism that would allow favouring patrlines within social insect colonies may arise because kin recognition molecules rub off, so everyone shares cues. The producer of such molecules may benefit even if it becomes as ignorant of relatedness as its colony-mates. Genes that enforce meiosis rules on all genes, including themselves, may fall in this category.

At the other extreme, many cases involve exploitation through ignorance. Social parasite queens fool the host workers by acquiring the colony odours of their hosts [11]. Though this leads to phenotypic cooperation and eliminates conflict, the host’s cooperation is not adaptive. It is an exploitative adaptation of the parasite. There is nothing parallel to the justice of Rawls’s veil of ignorance.

Many examples are intermediate, where one party gains by imposing ignorance while the other party loses fitness but still favours cooperation. A queen may be selected to lay indistinguishable male and female eggs, preventing workers from killing her sons. The workers lose inclusive fitness, but they still gain overall from raising the queen’s offspring, and the reduction in conflict may provide some benefit to all parties.

Cooperation based on ignorance could be defeated if cheaters can lift the veil. Cheaters are often thought of as subverters of information, chiefly in trying to avoid detection, but they can also gain by acquiring information to become smarter. However, the example of meiosis suggests that ignorance can be quite stable and may be an overlooked device supporting cooperation.

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References