

Red ants with green beards

In colonies of social insects such as ants, bees and wasps, only one or a small number of individuals function as fertile reproductive queens. The remaining female members of the colonies function as sterile workers who spend all or most of their lives assisting the queens to reproduce. Such altruistic behaviour on the part of the workers appears paradoxical from the point of view of the theory of natural selection because we expect genes responsible for altruistic behaviour to be rapidly eliminated. Hamilton (1964a,b) showed however that natural selection can favour the spread of altruistic alleles if altruism is directed preferentially towards close genetic relatives of the altruists. But how do animals recognize their relatives so that they can so direct their altruism? Although the publication of Hamilton's paper led to an explosion of studies on altruism, especially in the social insects, little attention was paid to the explicit question of recognition. Everyone assumed that relatives are recognized by the context in which they are encountered—ants that happen to be in the same nest must be close relatives.

A classic paper by Greenberg (1979) led to other studies demonstrating that social insects can recognize kin even outside the context of their nests. But it appeared that recognition operated via shared, environmentally acquired cues rather than because two individuals are genetically related (Gadagkar 1985; Fletcher and Michener 1987; Keller 1997). However, genes that can 'recognize each other' have long existed in the fertile minds of theoreticians. To quote Hamilton (1964a,b) "That genes could cause the perception of the presence of like genes in other individuals may sound improbable; at simplest we need to postulate something like a supergene affecting (i) some perceptible feature of the organism, (ii) the perception of that feature, and (iii) the social response consequent upon what was perceived." Dawkins (1976) drew widespread attention to these hypothetical genes with the words, "It is theoretically possible that a gene could arise which conferred an externally visible 'label', say a pale skin, or a green beard, or anything conspicuous, and also a tendency to be specially nice to bearers of that conspicuous label." Green beard genes have been discussed frequently in the literature but have generally been dismissed as unlikely for two kinds of reasons. One, to expect a single gene to confer a conspicuous label, make the bearers of this label recognize a similar label on other individuals and also make them behave differently towards such individuals seems unlikely. Second, even if a green beard gene did arise, it would soon go to fixation (Wade and Breeman 1994) so that everyone in the population would possess a green beard and we would then no longer recognize this as something special.

Now, Keller and Ross (1998) (see also Grafen 1998; Hurst and McVean 1998) have produced what appears to be the first experimental evidence for a green beard gene in polygynous colonies (colonies with many queens) of the so called red fire ant, *Solenopsis invicta*. This is an Argentinean ant that has been accidentally introduced into the United States and has gone on to become something of a pest. Keller and Ross (1998) were not really looking for a green beard gene; like many social insect researchers they were studying variable allozyme loci to determine genetic relatedness within and between ant colonies and populations. During this study they hit upon a locus, *Gp-9*, that has two alleles, *B* and *b*. Diploid individuals (all females,—queens and workers included are diploid) are expected to have one of the three genotypes, *BB*, *Bb*, *bb*. They found that *bb* individuals are very rare both among queens and workers, the reason being that they appear to die from intrinsic causes. *BB* individuals are found among workers and also among virgin (as yet non-reproductive) queens but are completely missing among reproductive queens. The heterozygotes *Bb* are however found both among queens and workers. Keller and Ross (1998) looked closely at the social dynamics of the colonies in an attempt to unravel the mystery of the missing *BB* queens. What they found was remarkable: all *BB* queens attempting to reproduce were killed, and they were killed primarily by workers of the genotype *Bb*. In other words, workers who possess at least one copy of the gene *b* kill reproductive queens that do not possess at least one copy of *b*. The recognition of *BB* queens appears to be due to a transferable odour cue because *Bb* workers involved in killing *BB* queens sometimes acquire the offending smell and themselves become victims of aggression by other *Bb* workers. Keller and Ross (1998) interpret *b* as a green beard gene itself, or as a gene that is closely linked to a green beard gene that

confers (i) an externally perceptible label (smell), (ii) the ability to recognize the presence and absence of this label on other individuals and (iii) the behavioural repertoire required to behave differently towards those who possess the label (not kill) and those that lack it (kill).

These findings raise many questions. Why should *Bb* workers kill only reproducing *BB* queens and not non reproductive ones? A plausible proximate answer to this question is that queens possess a smell that is correlated both with their reproductive activity and with their genotype. The 'ultimate' answer to this question is obvious differential long-term survival of the alleles *B* and *b* will be ensured by differential behaviour towards the reproducing queens (killing of non-reproductive individuals is, in this sense, of no consequence). Why were Keller and Ross (1998) successful at discovering a green beard gene (even if by accident) while others were not? Because of the fact that unlike what was predicted on theoretical grounds, this green beard gene has not gone to fixation. But why has it not gone to fixation? The answer, and thus the secret of Keller and Ross's success, seems to lie in the misfortune of the *bb* individuals who die prematurely. The only individuals who possess *b* and survive to carry on their crusade against *B* are the heterozygotes, who automatically also harbour a copy of *B*. Thus *B* can never be completely eliminated. It is because of this quirk that *b* has not gone to fixation and we still recognize it as a green beard allele and why Keller and Ross have succeeded where others have failed. This implies that hypotheses about genes programming individuals to recognize other individuals that carry the same gene, and to behave differently towards them, are not so far fetched after all. The findings underscore the point that the interplay between cooperation and conflict are to be expected at all levels of biological organization (Gadagkar 1997) and that their investigation requires us to shed our traditional compartmentalization into biochemists, ecologists, evolutionary biologists and so on and combine bold theoretical speculations and meticulous empirical investigations.

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