

Altruism, Spite, and Greenbeards

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Hamilton's theory of inclusive fitness showed how natural selection could lead to behaviors that decrease the relative fitness of the actor and also either benefit (altruism) or harm (spite) other individuals. However, several fundamental issues in the evolution of altruism and spite have remained contentious. Here, we show how recent work has resolved three key debates, helping clarify how Hamilton's theoretical overview links to real-world examples, in organisms ranging from bacteria to humans: Is the evolution of extreme altruism, represented by the sterile workers of social insects, driven by genetics or ecology? Does spite really exist in nature? And, can altruism be favored between individuals who are not close kin but share a "greenbeard" gene for altruism?

Darwin's (1) theory of natural selection explains both the process and the purpose of adaptation (Fig. 1). The process is that heritable characters associated with greater reproductive success will be selected for and accumulate in natural populations. This leads to the apparent purpose of adaptation: characters appearing as if designed to maximize the individual's reproductive success (fitness).

altruistic or spiteful traits, which are costly to the individuals that perform them. The paragon of altruism is the sterile worker caste within social-insect colonies, which help rear the offspring of their queen. An equally extreme example are slime mold cells that altruistically give up their own survival to become the nonviable stalk of a fruiting body, helping other cells to disperse in the form of spores (5). The problem is that such altruism

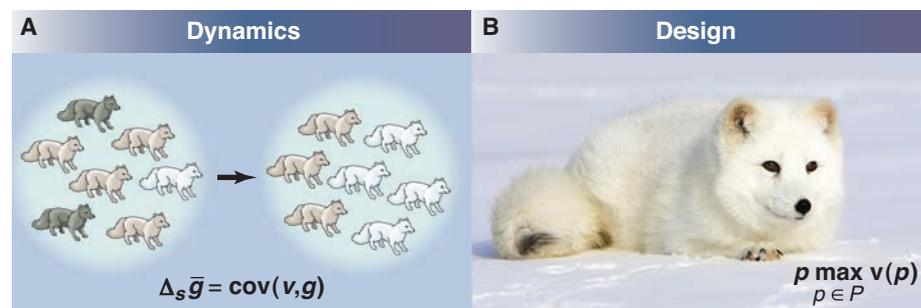


Fig. 1. Darwinian adaptation—dynamics and design. **(A)** Natural selection is the genetic change in the population owing to differential reproductive success of individual organisms. For example, among ancestral Arctic foxes, individuals with pale fur left more descendants than individuals with dark fur so that genes for pale fur accumulated in the population. Price's (35) equation formalizes this, stating that the change in the heritable portion of any character ascribable to natural selection ($\Delta_s \bar{g}$) is equal to the covariance between an individual's genetic ("breeding") value for the trait (g) and its relative fitness (v). **(B)** As a consequence of past natural selection, today's Arctic foxes look "designed" to fit their environment. This is captured by an optimization program, which states that the phenotype (p) of the organism is functioning as if to maximize the individual's relative fitness (v ; more generally, its inclusive fitness) (6, 7). [Credit: Biosphoto/Cordier Sylvain/Peter Arnold Inc.]

Fisher (2) united Darwinism with Mendelian genetics by describing natural selection in terms of changes in gene frequencies. Genes associated with greater individual fitness are predicted to increase in frequency, leading to an increase in mean fitness. This "fundamental theorem of natural selection" was intended to capture the process (natural selection) and the purpose (maximization of individual fitness) of adaptation.

Altruism, Spite, and Inclusive Fitness

In the 1960s, Hamilton (3, 4) realized that maximization of individual fitness could not explain

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reduces the reproductive success of the altruist—so why is it not weeded out by natural selection?

Hamilton (3) showed that genes can spread not only through their direct impact on their own transmission but also through their indirect impact on the transmission of copies present in other individuals. Consequently, altruistic behaviors can be favored if the benefits are directed toward other individuals who share genes for altruism (Fig. 2). This is encapsulated by Hamilton's rule (3), which states that a trait will be favored by selection when $rb - c > 0$, where c is the fitness cost to the actor, b is the fitness benefit to the recipient, and r is their genetic relatedness. This form of Hamilton's rule emphasizes interactions between two individuals, but it can be extended to allow for interactions with multiple individuals [supporting online material (SOM) text and table S1].

Hamilton's general point was that natural selection leads organisms to appear designed as if to maximize their inclusive fitness, which is the sum of fitness gained through producing offspring (direct fitness) and through affecting the fitness of related individuals (indirect fitness). The easiest way in which indirect fitness can be obtained is through interactions with close kin, in which case genes are identical by descent (from a common ancestor), and so this is usually referred to as "kin selection." However, inclusive fitness is not simply a concept that relates to interactions between relatives; it is our modern interpretation of Darwinian fitness, providing a general theory of adaptation (6, 7).

Extreme Altruism and the Haplodiploidy Hypothesis

The sterile workers of the social insects are extreme altruists, who give up any chance of independent reproduction in order to help others. In the Hymenoptera (ants, bees, and wasps) and termites, this extreme altruism has led to a division of labor between individuals and the evolution of the highest level of social organization, termed eusociality. Depending upon how eusociality is defined, it has evolved 3 to 11 times in the Hymenoptera, as well as in termites, thrips, aphids, spiders, beetles, shrimps, and mole rats (8, 9).

A major topic of debate has been whether eusociality has evolved multiple times in hymenopterans because of their haplodiploid genetics or their ecology. Under haplodiploidy, fertilized eggs develop into (diploid) females, and unfertilized eggs develop into (haploid) males. Hamilton (3) suggested that because haplodiploidy leads to a female being more related to her sisters ($r = 0.75$, assuming an outbred population in which females mate once) than her own offspring ($r = 0.5$), this makes it easier for Hamilton's rule to be satisfied (Fig. 3A).

However, haplodiploidy also leads to a female being less related to a brother ($r = 0.25$), exactly canceling the benefit of increased relatedness to sisters (10). The haplodiploidy hypothesis is not rescued if the population sex ratio is biased toward females because this bias also reduces the relative reproductive value of females, exactly canceling any relatedness benefits (11). Numerous studies have examined whether certain life histories could rescue Hamilton's haplodiploidy hypothesis by making the average relatedness to siblings $r > 0.5$, but none appears generally applicable (SOM text). In contrast, others have argued that what is special about the hymenopterans is that their natural history leads to a relatively high benefit of helping (high b/c ratio), such as advanced parental care and a powerful sting that facilitates group defense (12).

The Monogamy Hypothesis

Recent work (8, 13) has suggested a possible resolution to this debate, arguing that strict lifetime monogamy, in which females only mate with

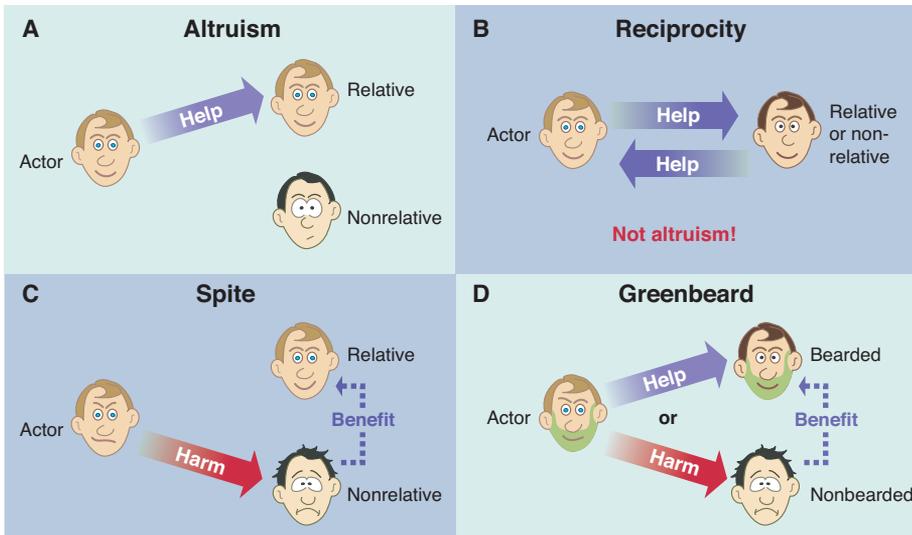


Fig. 2. Mechanisms for altruism, spite, and reciprocity. **(A)** Altruism can be favored if it is preferentially directed toward relatives. **(B)** Reciprocity is favored when it makes the actor more likely to receive help in the future. Reciprocity relies upon a future direct fitness benefit for cooperation and so is not altruistic. **(C)** Spite can be favored if it is preferentially directed toward relatively unrelated individuals, whose loss improves the fitness of relatives. **(D)** Greenbeards are favored by directing altruism toward fellow greenbeard individuals or spite toward nonbearded individuals.

one male in their entire life, is crucial for the evolution of eusociality. Monogamy leads to a potential worker being equally related ($r = 0.5$) to her own offspring and to the offspring of her mother (siblings). In this case, any small efficiency benefit for rearing siblings over their own offspring ($b/c > 1$) will favor eusociality (Fig. 3B).

In contrast, even a low probability of multiple mating means that potential workers would be more related to their own offspring. In this case, costly helping would require a significant efficiency advantage to rearing siblings over own offspring (Fig. 3C). Until group living is established, allowing the evolution of specialized cooperative behavior and division of labor, the ratio b/c cannot be expected to greatly exceed 1. For example, feeding a sibling is unlikely to be hugely more beneficial than feeding an offspring by the same amount. Consequently, in the absence of strict monogamy the population cannot even get started on the road to eusociality.

In support of this hypothesis, comparative studies have found monogamy to be the ancestral state in all the independent origins of eusociality studied (9, 14). Monogamy originated first, giving a high relatedness, and then when ecological conditions led to a high enough b/c , eusociality evolved (SOM text). Important ecological conditions include “life insurance” benefits of allowing helpers to complete parental care after the death of the mother (for example, ants, bees, and wasps), and “fortress defense” benefits of remaining to help use or defend a food source, when opportunities for successful migration are low (for example, aphids, beetles, termites, thrips, and shrimps) (12, 14).

There are some eusocial species in which queens mate multiply. However, this is a derived condition that has evolved after workers have

already lost the ability to mate and realize full reproductive potential (9). Furthermore, these species have had the time to evolve division of labor and specialized helping behaviors, giving a substantial b/c .

The beauty of the monogamy hypothesis is that it simplifies our understanding of how eusociality evolved, emphasizing that the interaction between kinship and ecology is fundamental and that they are not competing explanations (8, 13). For example, the search for how to increase relatedness

to siblings ($r > 0.5$) has been a red herring; what is key is that average relatedness stays at 0.5. Other red herrings include the possibility for eusociality to have evolved via cooperation between sisters (the parasocial route) because that would lead to $r < 0.5$ (8) and the suggestion that high relatedness is a consequence rather than a cause of eusociality (15), in which case the observed correlation with monogamy would not be predicted (9). Finally, the monogamy hypothesis suggests that factors that facilitate monogamy, such as lifetime storage of sperm by females, are also important in explaining the distribution of eusociality.

Get the Right Spite

Inclusive-fitness theory explains altruism but also has a darker side. Spiteful traits, which are harmful to both actor and recipient, may be favored (4). Considering the classic two-party version of Hamilton’s rule, if c is positive (which is costly to the actor), and b is negative (which is costly to the recipient), then $rb - c > 0$ can be satisfied if relatedness (r) is negative. Negative relatedness may seem a bizarre concept, but it simply means that the recipient is less related to the actor than is an average member of the population (SOM text).

Another way to think about spite is to distinguish between the primary recipient of the harming behavior (the individual physically attacked) and those secondarily influenced as a byproduct of this (those experiencing reduced competition from the harmed individual) (16, 17). From this perspective, spite can be favored if the actor is more related to the secondary recipients (who benefit) than to the primary recipients (who are harmed). Spite can therefore be thought of as altruism toward the secondary recipients: Harming an individual can be favored if this provides a

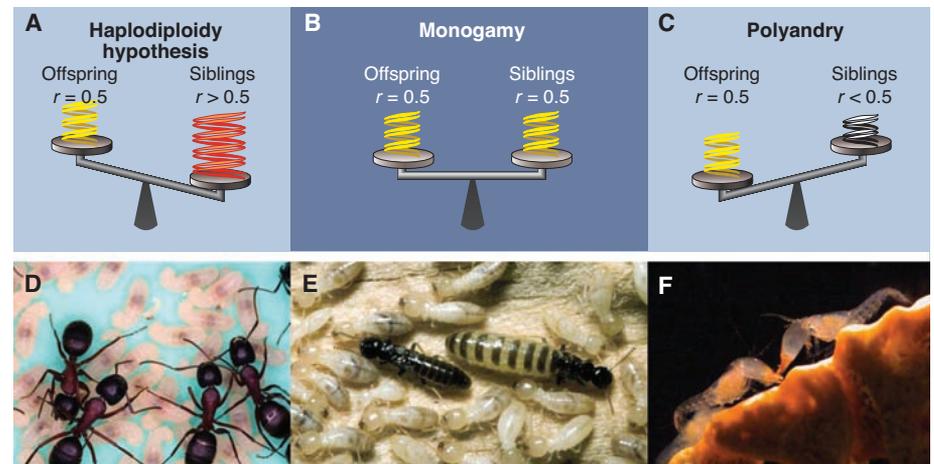


Fig. 3. Monogamy paves the way to eusociality. **(A)** The haplodiploidy hypothesis relies on individuals being more related to siblings than offspring, making siblings worth more than offspring. As originally envisioned, this appears to have been a red herring. **(B)** The monogamy hypothesis emphasizes that if an individual is equally related to its siblings and its offspring, even a very slight efficiency benefit for raising siblings translates into a selective advantage for helping. **(C)** Without strict monogamy, individuals are more related to their offspring than they are to their siblings so that a large efficiency benefit is required in order for sibling-rearing to be favored. **(D)** Sterile workers caring for brood in the ant *Camponotus herculeanus*. **(E)** A lifetime monogamous pair from the termite *Reticulitermes flavipes*. **(F)** Nonbreeding workers in the shrimp *Synalpheus regalis*. [Photos provided by David Nash, Barbara Thorne, and Emmett Duffy]

benefit to closer relatives (Fig. 2C). These two different encapsulations of spite are different ways of looking at the same thing, using either a two- or three-party Hamilton's rule (SOM text) (16, 17). If the actor is more closely related to the secondary recipients than the primary recipients in a three-party rule, then this leads to a negative relatedness in the two-party rule.

Although many behaviors have been suggested as spiteful, they are usually explained as selfish behaviors that are costly to the recipient but provide a benefit to the actor ($c < 0$) (Table 1). This benefit is often a reduction in future competition for resources, for the actor or their offspring, with confusion arising because the direct fitness consequences were only considered in the short term and not over the lifetime of the actor (SOM text) (18). What matters for natural selection are fitness consequences over the entire lifetime and not some arbitrary period. For example, herring gulls kill the chicks at neighboring nests, but this reduces the future competition over resources for both themselves and their offspring. Furthermore, there is no evidence that such examples involve a sufficient secondary benefit to relatives. Indeed, it has even been suggested that the conditions required are so restrictive that spite would be rare or nonexistent (11, 12).

However, recent theory has shown that a positive relatedness to secondary recipients can be obtained more easily than previously thought, suggesting that at least from a theoretical perspective spite is plausible (19) if there is (i) large variance in relatedness between competitors; (ii) kin discrimination, with harming behaviors aimed at individuals to whom the actor is relatively unrelated (making the actor relatively more related to the secondary recipients); or (iii) strong local competition so that harming the primary recipient provides appreciable benefits to secondary recipients. When these conditions are met, spiteful behaviors can be favored so as to reduce competition for relatives. Consider the extreme example of when two genetically identical (clonal) individuals are competing with a nonrelative to whom they are unrelated. One of the clone-mates could be selected to harm the nonrelative, at a cost to itself, if this harming reduces the nonrelative's ability to compete for resources and hence benefits the other clone-mate.

Real Spite

To demonstrate spite, it must be shown that a trait is costly to the actor (positive c) and costly to the recipient (negative b). In addition, for spite to have evolved by means of natural selection, the actor must be more closely related to the secondary recipients (beneficiaries) than to the primary recipient that they harm (Fig. 2C). The

Table 1. Not spite: examples of traits that have been suggested as spiteful but actually provide a direct benefit to the actor and hence are selfish (table S2).

Taxa	Suggested spiteful traits	Why selfish, not spiteful
Birds	Protection of territories, siblicide at neighboring nests.	Decreased competition for resources, for self or offspring
Fish	Egg cannibalism	Decreased competition for resources, for offspring
Humans	Punishment and rejection of low offers in economic games	Leads to increased cooperation in the long term
Mammals	Infanticide, harassment of nondescendant juveniles and injured males	Decreased competition, for offspring or mates

sterile soldier caste in polyembryonic parasitoid wasps satisfies all these conditions (17). Females lay their eggs on the eggs of moth caterpillars, after which the wasp eggs divide asexually and consume the growing caterpillar from the inside (20). Although most larvae develop normally, a fraction become a soldier morph. Developing as a soldier is costly to the actor, because the soldiers are sterile, and costly to the recipient, because the soldiers seek out and kill other larvae within the host. Finally, soldiers preferentially kill larvae to which they are less related (those that have developed from other eggs), freeing up resources for their clone-mates.

Another example of spite is provided by the production of antimicrobial bacteriocins by many bacteria (21). These compounds are lethal

to conspecifics that lack an immunity gene (22). In some cases, cell death is required to release the bacteriocins into the environment, and so it is clearly a costly trait (positive c). In addition, there is genetic linkage between the bacteriocin production and immunity genes so that close relatives both produce and are immune to a particular bacteriocin (22). Consequently, the release of bacteriocins kills nonrelatives, freeing up resources for clone-mates. Experimental work on bacteriocins has also supported the prediction that the relative advantage of spite is greater when variance in relatedness is higher (giving

an intermediate mean relatedness) because this leads to interactions with both close relatives and nonrelatives, allowing a relatively higher relatedness to the secondary beneficiaries (Fig. 4) (21, 23).

Spiteful Words

As discussed above, spite can be considered a form of altruism. Consequently, it is useful to ask whether we gain anything by distinguishing spite from altruism. At one level, it can be useful to emphasize the similarities, that both are favored because they lead to an increase in the inclusive fitness of the actor through indirect fitness consequences. This will also help avoid debates over whether certain traits should be classed as altruism or spite because the mathematics of any

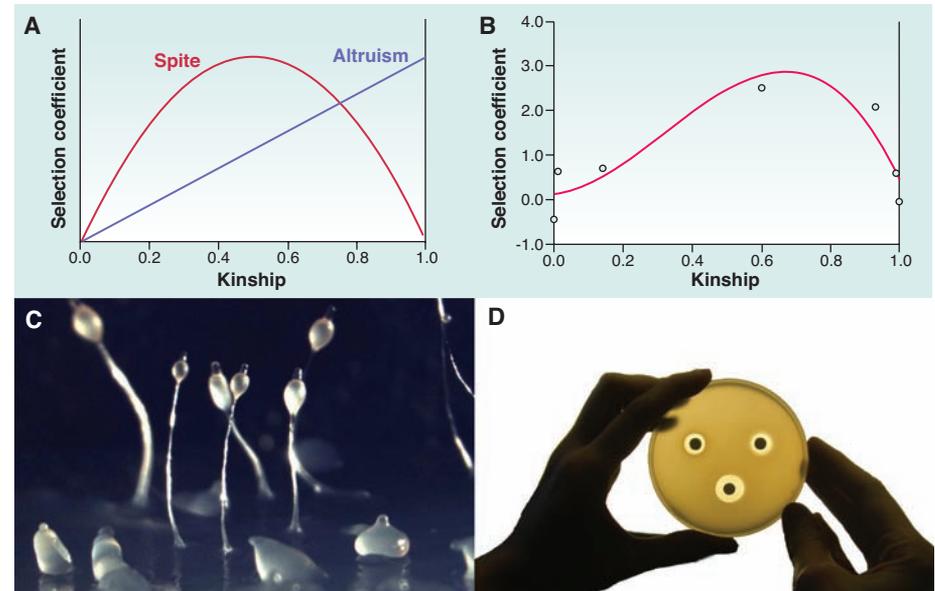


Fig. 4. Population structure, altruism, and spite. (A) Theory predicts that as relatedness within a patch increases, there is an increase in altruistic traits and a domed relationship with spiteful traits (3, 15). (B) As predicted, the relative benefit of bacteriocin production in *Pseudomonas aeruginosa* shows a domed relationship with relatedness (23) (C) Altruism: a fruiting body of the slime mold *Dictyostelium discoideum*. (D) Spite: A piece of filter paper soaked with a bacteriocin (left spot) causes an inhibition zone where bacteria cannot grow, in the same way as a traditional antibiotic (right spot; bottom spot shows both in combination). [Photos provided by Owen Gilbert, Margaret Riley, and Sara Cody]

case can be rearranged so as to make a spiteful or altruistic two-party rule (16, 17).

However, there are also a number of reasons why it is useful to distinguish spite from altruism (17). From a behavioral perspective, there is a clear difference between helping and harming. Additionally, there are biologically interesting differences between altruism and spite. For example, local competition for resources typically selects for spite and against altruism (21); altruistic traits are predicted to show a positive relationship with relatedness (3), whereas spiteful traits are predicted to show a domed relationship (Fig. 4) (19, 21); and kin discrimination is key in the examples of spite, whereas altruism can often evolve without kin discrimination when limited dispersal keeps relatives together (3).

Spite can also be defined from a mechanistic or psychological perspective in primates and humans as a behavior that harms another or arises from a desire to harm another (24, 25). In these cases, harming is likely to be favored because on average it provides a direct benefit to the actor ($c < 0$) and is selfish, not spiteful. It is crucial not to mix definitions of spite by raising the problem and rarity of evolutionary spite then going on to examine a harming behavior that provides a direct benefit to the actor, and therefore is not evolutionary spiteful. The specific conditions required to favor evolutionary spite might make it relatively unlikely in humans and other primates. Indeed, spite may be rare in general because it is hard to obtain situations in which populations are structured so that harming nonrelatives is an efficient way of helping relatives.

Greenbeards

Hamilton (3, 26) pointed out that indirect-fitness benefits require genetic relatedness per se and not kinship. Imagine a gene (or cluster of tightly-linked genes) that gives rise to a conspicuous phenotype, uses this phenotype to discriminate between carriers and noncarriers of the gene, and leads to costly helping toward other carriers of the gene (Fig. 2D). This gene could be favored by natural selection, even if carriers share no other genes in common. Thus, the crucial requirement for altruism is genetic relatedness at the altruism locus and not genealogical relationship over the whole genome.

Dawkins proposed the hypothetical example of a gene that gives rise to a green beard while simultaneously prompting individuals with green beards to direct cooperation toward other green-bearded individuals (27). However, this “greenbeard” mechanism can also occur without a visible tag. What is required more generally is a single gene (or a number of tightly-linked genes) encoding both the cooperative behavior and causing cooperators to associate (26, 28). Greenbeards are one of the two ways in which natural selection can favor altruistic behavior, with the other being interactions with genealogical kin (3). However, despite this fundamental position it has been assumed that greenbeards

would not occur in nature because they could be easily invaded by “falsebeards” (cheats) that displayed the beard without also performing the behavior (27).

This assumption has been overturned by the discovery of a number of altruistic greenbeards. In the slime mold *Dictyostelium discoideum*, individuals with the *csa* gene adhere to each other in aggregation streams and cooperatively form fruiting bodies while excluding noncarriers of the gene (5). Other examples have been found in yeast, a bacterial plant pathogen, and a lizard (SOM text). In addition, spiteful greenbeards have been discovered, including the *Gp-9* gene of the fire ant *Solenopsis invicta* (29). Workers with the *b* allele at this locus use odor to determine whether prospective queens also carry this allele, dismembering them if they do not. Another example is provided by bacteriocin production, in which the bacteriocin-encoding gene and the immunity gene are tightly linked (22).

Theoretical work has clarified when we would expect greenbeards to occur (30). Greenbeards can be categorized into four groups, with different evolutionary dynamics, according to whether they are altruistic (helping) or spiteful (harming) and always expressed (obligate; for example, bacteriocins) or only expressed in response to the presence of the greenbeard in others (facultative; for example, *Gp-9*). For all cases except the facultative altruistic greenbeard, the greenbeard is selected against at low frequencies and only favored when it has established itself to a certain frequency. Population structure can solve this problem by keeping individuals with greenbeards together. The best place to look for new greenbeards may be in microbes, in which asexual growth can lead to extreme population structuring; the relatively simple link between genotype and phenotype may prevent a decoupling of beard and social trait (falsebeards), and genetic knockouts facilitate the detection of greenbeards (30).

Some models for altruism in humans (31–34) and social insects (15) implicitly invoke greenbeard mechanisms without realizing this, such as the suggestion that altruistic individuals differ from individuals who are not altruistic in some observable characteristic [such as being more likely to smile and laugh (31, 32)] or models of “strong reciprocity” that assume punishment and altruism to be genetically linked (33, 34). However, there is no reason to suspect that traits such as smiling or punishment will be encoded by the same gene or closely linked genes as those that lead to altruism. Consequently, falsebeards could arise, and these proposed explanations for altruism would not be evolutionarily stable (30).

Conclusions

A unifying theme in all the issues that we have discussed here is the importance of the interplay between theory and data. The monogamy hypothesis cuts through the superfluous details by focusing on a key aspect of the underlying

biology. Theoretical work on spite and greenbeards was spurred by biological examples but then led to a unifying framework that illuminated detection problems and suggested where to look for further examples. All of these examples illustrate that the distinction between genetics (*r*) and ecology (*b/c*) is both artificial and unhelpful. What really matters is how they interact, as has always been emphasized by Hamilton’s rule.

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Supporting Online Material

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SOM Text
Tables S1 and S2
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This PDF file includes:

SOM Text

Tables S1 and S2

References

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In this section we expand in greater detail upon several issues we address in the main text, clarifying links with the existing literature more generally.

Hamilton’s rule

Hamilton’s rule ($I, 2$) is usually written as $rb - c > 0$, or in some equivalent form, which emphasizes a fitness interaction between a single actor (who suffers a fitness decrement c) and a single recipient (who gains a fitness increment b). However, actions will typically have fitness consequences for more than one recipient, so more generally we can write $\sum_{i \in I} r_i b_i - c > 0$, where I is the set of all individuals (excluding the actor) whose fitness is affected by the action ($b_i \neq 0$) and who are positively or negatively related to the actor ($r_i \neq 0$), and r_i and b_i are the relatedness and fitness increment, respectively, corresponding to the i^{th} recipient. Typically, costs and benefits are framed in absolute (surviving offspring) or relative (share of population reproductive success) terms. In scenarios where individuals belong to separate classes, such as sex or age classes, fitness effects must be expressed in terms of reproductive value (3-5). Note that this summation form is still Hamilton’s rule, and it would be pointless to argue, for example, that Hamilton’s rule is invalidated when there is more than one recipient. Rather, the key elements of Hamilton’s rule are: (1) the notion that a positive inclusive fitness effect is the ultimate criterion for an action to be favoured by natural selection; (2) that inclusive fitness is given by the sum of direct fitness and indirect fitness; and (3) that fitness effects for recipients are translated into indirect fitness effects for the actor in proportion to the genetic relatedness of actor and recipient.

Nevertheless, it is worthwhile to ask: when does the simpler two-party rule $rb - c > 0$ exactly predict the direction of change in gene frequencies? It does so when the action has a single primary recipient to which the actor is positively or negatively related, and when secondary recipients are either absent or unrelated to the actor. In an infinite population, with either no or global regulation of density *in response to the social action*, secondary fitness consequences are either absent or shared among individuals whose relatedness to the actor is zero. In a finite population, the social action only gives a net secondary indirect fitness effect of zero if there is no density regulation effect for other individuals. This is because the secondary recipients will generally not have an average relatedness of zero to the actor. Exceptional cases exist in principle: where density regulation falls unevenly on the other individuals in the population, and in a contrived way in relation to their relatedness to the actor, so as to give a secondary indirect fitness effect of exactly zero; or else, slightly more plausibly, where the recipient is related to the actor by $r = -1$, so the remainder of the population is related to the actor, on average, by zero. Note that, if we choose to measure costs and benefits in relative-fitness or reproductive-value terms, then density regulation is unavoidable as, for one individual to gain, other individuals must lose, and *vice versa*. These considerations reveal that, in very many cases, the indirect fitness effects of social actions owing to their impact on secondary recipients cannot be ignored, and two-party Hamilton’s rules will be the exception rather than the rule.

The haplodiploidy hypothesis

Hamilton (2, 6) suggested that, because haplodiploidy leads to a female being more related to her sisters ($r=0.75$, assuming an outbred panmictic population where females mate once) than her own offspring ($r=0.5$), this makes it easier for Hamilton's rule to be satisfied. This has become known as the haplodiploidy hypothesis.

Trivers & Hare (7) pointed out that this doesn't necessarily hold, because haplodiploidy also leads to a female being less related to a brother ($r=0.25$), which exactly cancels the benefit of increased relatedness to sisters. They suggested that the haplodiploidy hypothesis could still hold if the sex ratio was biased towards females to whom the workers would be more related (their sisters).

Craig (8) showed that this also wouldn't work, because a female biased sex ratio would make the relative reproductive value of females lower than that of males, to the extent that this exactly cancels any relatedness benefit.

A number of workers have since shown that the haplodiploidy hypothesis can still be rescued if the workers are able to disproportionately help sisters, but the population sex ratio is not biased. For example, if there are split sex ratios, or if workers preferentially help sisters. This can happen through a number of possible life histories, although there is no evidence that any of them are of general importance (9-15).

Can the haplodiploidy hypothesis be rescued by worker production of sons? Charnov (16) showed that the haplodiploidy hypothesis could not be rescued by workers simply producing sons. This is because the relatedness to sons is the same as the mean relatedness to sisters and brothers ($r=0.5$). The haplodiploidy hypothesis can be rescued by worker production, but only with the additional complexity that workers distinguish between brothers and sisters and specifically substitute sons for brothers. However, he argues that this is unlikely to be important because it would require the simultaneous evolution of helping and being able to determine sex of siblings. This is unlikely because there would be no selection for the ability to determine the sex of siblings until helping had already evolved.

Can the haplodiploidy hypothesis be rescued by maternal effects? Maternal effects are when phenotypes are influenced by the genotype of the mother as well as the genotype of the individual being examined. Wade (17) showed that maternal effects which benefit the mother but not the offspring can spread more easily in haplodiploids. This suggests that the parental manipulation hypothesis (18), that that eusociality could arise by parents coercing some young into becoming helpers, such as through reduced fertility, may occur more easily in haplodiploids.

The monogamy hypothesis

Boomsma (19, 20) was not the first to highlight the significance of monogamy, but the merit of his reformulation of this idea with explicit emphasis on life-time monogamy is that it can be explained in very simple terms. Historical details can be found in Boomsma's (19, 20) papers.

The ecological correlates of cooperation and eusociality

A number of studies have examined the ecological correlates of cooperation and eusociality.

In the eusocial insects it has been suggested that ecological advantages of cooperation and eusociality arise from two factors (21, 22). First, there can be a substantial benefit to staying at the natal nest and helping defend a valuable resource. This advantage of “fortress defense” is likely to be important in species which live in protected, expandable sites, where food is obtained, such as the wood galleries of termites and the plant galls of social aphids and thrips. Remaining to help at the natal ‘fortress’ avoids the risk of death associated with migration, and because food is available locally, little feeding care is required, the first worker specialists are generally soldiers, specialized for defence.

Second, there can be a ‘life insurance’ benefit in species where the adults must leave the nest to forage for food to feed their dependent young (23, 24). In these species, when multiple individuals help raise the larvae, this allows parental care to be completed even if one or more adults die. This insurance benefit is likely to be key in species such as ants, bees and wasps, and has been experimentally supported in a tropical hover wasp (25).

In mole-rats, solitary species tend to live in mesic habitats with a well-balanced supply of water, whereas the eusocial species live in arid areas where rainfall is low and unpredictable (26). In the latter kind of habitat, food resources are patchy making foraging more risky, and harder soil means that the energetic cost of foraging (burrowing) is higher. Across all mole-rat species, larger groups are associated with a lower density of food (underground roots and swollen tubers of plants) and a greater variation in rainfall (26).

In sponge-dwelling shrimps, it has been argued that competition for host sponges, which provide both habitat and food is a key ecological factor driving the evolution of cooperation and eusociality (27). Extreme competition for sponges reduces the benefit of dispersing to breed independently (ecological constraints), and increases the benefit of staying to help defend the natal patch. This is analogous to ‘fortress defense’, discussed above.

In birds, cooperatively breeding species tend to live in regions where the winters are warm and the variation in temperature is low, thus enabling species to become sedentary and maintain territories all year round (28, 29). This provides support for the idea that cooperation is favoured when available breeding sites are limiting (habitat saturation), because it would lead to year round competition for breeding sites. Considering life history variables, cooperative breeding species tend to have lower mortality rates and lower rates of dispersal, which could also lead to greater competition for territories (28, 29). In many bird cases, helping may represent the best of a bad job, in response to factors such as failed breeding attempts (30) or a lack of suitable nesting sites (31), and so the b/c ratio can be very high due to a low c .

Social behaviours and intentional language

From an evolutionary perspective a trait or behavior is social if it has fitness consequences for both the individual that performs that behavior (the actor) and another individual (the recipient). Hamilton (2) classified social behaviors according to whether the consequences they entail for the actor and recipient are beneficial (increase direct fitness) or costly (decrease direct fitness) (Table SOM1).

The adaptationist approach provides the formal justification for the use of intentional language, such as altruism and spite (32). Specifically, the dynamics of natural selection leads to individual organisms that behave as fitness maximizing agents, and hence behave as if they have intention or purpose at the individual level. Intentional terms do not provide a superficial gloss, but rather convey important information about gene frequency dynamics. In particular, the maximizing agent analogy has been formalized with respect to an individual's lifetime reproductive success – not for just some aspect of fitness (e.g. fecundity) or over some limited time scale or relative to some subset or group of the population.

Alternative evolutionary definitions of terms such as altruism both cause confusion and lack a formal justification (33). For example, the use of 'reciprocal altruism' defines altruism over the short-term fitness consequences. However, natural selection operates on lifetime fitness consequences, not over some arbitrary short-term. Reciprocal altruism is not actually altruistic (Fig. 2), and so better termed reciprocity' (33). To give another example, the group selection literature defines altruism relative to the fitness of other individuals in the group (34). However, natural selection operates on fitness relative to the population, not some arbitrary fraction of it. These and other examples are discussed in greater detail in the following section.

Effect on actor	Effect on recipient	
	+	-
+	Mutually beneficial	Selfish
-	Altruistic	Spiteful

Table SOM1. Social Behaviors. An evolutionary classification scheme for social behaviors that have been selected for by natural selection (2, 33). Effects are measured in terms of lifetime effects on direct fitness. Helping behaviors are + to the recipient, and can be mutually beneficial or altruistic. Harming behaviors are – to the recipient and can be selfish or spiteful. Cooperation is defined as a helping behavior that has evolved at least partially due to the effect on the recipient – this includes all altruistic behaviors and some mutually beneficial behaviors (33). Most social behaviors will have fitness consequences for three or more individuals, so we may say that a behavior is altruistic in relation to impact upon one recipient, and spiteful in relation to its impact upon another recipient. It is reasonable to term such a behavior as altruism if the primary recipient is the beneficiary, and spite if the primary recipient is the victim.

Not altruism

Terms such as altruism have very specific meanings, which convey useful information. If these terms are misused, or redefined, the result is confusion (33). This has been a particularly large problem with the term altruism (33), p. 419-423), which has been redefined in many ways, including: (a) reciprocal altruism, where helping is favoured because it will lead to the actor being helped back at a later date (35); (b) a decrease in the fitness of the focal individual, relative to the other members of its group (relatively costly to individual, relatively beneficial to the group; sometimes termed 'weak altruism') (34, 36-41); (c) a decrease in fitness over the short term (42, 43); (d) playing cooperate in a prisoners' dilemma game (44); (e) a failure to harm others (45); (f) the mechanism by which one individual is motivated to help others (46).

The problem with all of these redefinitions is that they include situations where cooperation could provide a direct fitness benefit, and hence could be mutually beneficial. Consequently, this leads to a behavior being labeled as altruistic when it isn't costly and actually benefits the actor. For example, considering reciprocal helping (example a above), cooperation is only favored (between non-relatives) if it leads to an overall benefit (through increased likelihood of being helped in the future), in which case it is mutually beneficial, and so reciprocal altruism is not altruistic. In the other cases (examples b-f) helping can be mutually beneficial or altruistic (-/+), depending upon model details and parameter values assumed. Elsewhere, we discuss in detail the confusion that this can lead to (33). Such redefinitions obscure the fundamental distinction between when direct or indirect fitness benefits are required to explain the observed cooperation (33, 47, 48). This can lead to the situation where a behavior is described as altruistic, but can be explained by direct fitness benefits (i.e. by self-interested or self-regarding behaviors). More formally, these redefinitions are misleading because the spread of a gene is determined by its overall (lifetime) fitness consequences, relative to others in the breeding population, and not its consequences over some arbitrarily defined 'short-term', or relative to some subset of the population, such as with whom they happen to interact (4, 33, 49, 50).

It is also worth comparing the distinction between altruism and the various redefinitions with Boomsma's (19, 20) emphasis of the importance of the distinction between obligate and facultative eusociality (51). As long as eusociality is not obligate (i.e. every member of a helper caste is affected) there is still a (albeit often faintly minor) direct fitness interest to be had in the future from switching developmental pathway to personal breeding. This is why Boomsma categorizes facultative eusociality under cooperative breeding.

Spiteful or selfish?

There are numerous examples of harming traits which have been argued to represent evolutionary (or Hamiltonian) spite, but which can be explained by direct benefits to the actor, and which therefore represent selfish not spiteful traits (52, 53). In table SOM2 we summarize a number of examples, going into greater detail than in table 1. For many of these cases, the fact that the trait can be explained by direct benefits has already been pointed out. We would like to emphasize the additional point, that in all of these cases, there is no evidence that the harm caused by these traits provides a benefit to secondary recipients to who the actor is more closely related than the primary recipient (i.e. there is an appreciably negative relatedness).

In many of these examples the direct benefits to the actor of the trait are made explicit. For example "The primary impetus for infanticidal behavior is the elimination of offspring of other individuals to increase the probability of representation of one's own off- spring in the subsequent generation" (54). In such cases, the mislabeling as spite seems to follow from a lack of appreciation that the characterization of behaviors depends upon their overall (total or long-term) fitness costs to the actor, and not some arbitrary energetic or other cost measured over a short-term period. Another key point is that what matters is the average consequences of a trait, not individual cases. This is because the classification is based upon fitness consequences, and natural selection acts on the average fitness consequences of a trait. For example, suppose that aggression was

favored towards non-cooperative individuals to make them more likely to cooperate with the actor in the future. In this case, the aggression is favored because it is on average selfish, and it would be wrong to label it as selfish when it worked and spiteful when it didn't lead to a change in behavior. Finally, we also stress that the classification scheme is for traits that have been selected for by natural selection, and not strategies that are not selected in theoretical games, as our aim is to explain the existing diversity.

In two of the cases given in table SOM2, it is possible that the trait is sometimes performed spitefully. Further work is required to clarify these cases. First, Brereton (55) suggests the possibility that, whilst there will usually be return benefits to the sexual interferer (e.g. see p. 133-134), it is also possible that: "However, in stumptail macaques, where individuals of all age-sex classes participate, interference may be spiteful, inflicting a cost on the intruder and enough stress upon the mating male and female to delay conception, and may ultimately contribute to an intruder receiving a return benefit. Immatures may be participating on behalf of their mature kin." If immatures are interfering to increase the reproductive success of elder relatives, this would be spiteful. Second, it is theoretically possible that parasite-infected hosts could be favored to act in a way which increases the likelihood that non-relatives are infected, and hence decrease the competition for resources encountered by relatives (56, 57). However, we know of no empirical example that could fit this.

Wallace (58) discusses whether misinformation (deception) can be favored by natural selection and suggests that his analysis complements Hamilton's (59) analysis of selfish and spiteful behaviors. The examples he then gives, such as nuptial feeding, are more likely to be driven by selfish benefits. However, it is possible that deception could be favored as a spiteful trait, and Wallace emphasizes the need to limit misinformation to unrelated members of the population.

Organism	Trait	References	Why selfish and not spiteful
Birds	Protection of territories	(60-62)	Reduced competition for resources
Herring gull (<i>Larus argentatus</i>) and western gull (<i>L. occidentalis</i>)	Siblicide at neighbouring nests	(63, 64)	Reduced competition for resources
Humans	Punishment and rejection of offers in ultimatum game	(65)	In natural conditions, would lead to increased cooperation in long term
Humans	Contributing less than predicted in an economic game	(66, 67)	Individuals are maximizing relative payoff, and/or perceive other

			individuals in their group as competitors.
Macaques (several species)	Harassing infant and juvenile daughters of others	(68)	Reduced competition for own offspring
Macaques (stumptail, <i>Macaca arctoides</i>)	Sexual interference	(55)	Increased reproductive success in long term
Mammals	Infanticide	(54)	Reduced competition for own offspring
Monkeys (Old World)	Oestrous advertisement	(69, 70)	Honest signal of quality
Mountain sheep (<i>Ovis Canadensis</i>)	Harassing injured male	(68)	Increases chance the harassed male dies, and so reduces competition for mates in next breeding season
Parasite hosts	Decreased transmission of parasites	(56, 57)	No non-relatives of same species are being harmed, so it is a helping altruistic trait, not a harming spiteful trait
Sticklebacks	Egg cannibalism	(64, 71)	Reduced competition for own offspring
Theoretical	Aggression	(72)	More aggressive individuals are less likely to be attacked in the future
Theoretical	Defect in the prisoner's dilemma	(73)	Exploitation of cooperators

Table SOM2. Selfish not spiteful. Examples of traits which have been suggested as spiteful, but actually provide a direct benefit to the actor, and are hence selfish (52, 53). This table provides further details of the examples given in table 1.

Further examples of spite

Several other traits have been suggested as possible examples of spite. These include: worker policing and sex-ratio manipulation in the social insects (53); sperm competing for eggs (74); other forms of antagonism between microbes. Spite is likely to be less common than altruism, because it is hard to obtain situations where relatedness is sufficiently negative that harming non-relatives is an efficient way of helping relative

Hamiltonian versus Wilsonian Spite

A number of authors have distinguished Hamiltonian (59) from Wilsonian (75) spite (53, 65, 76, 77). In these cases, Hamiltonian spite is defined as when a harming trait is favored because it is directed towards negatively related individuals, and Wilsonian spite as when a harming trait is directed towards individuals whose reduced reproductive success provides an indirect benefit towards relatives. However, as we have stressed in the main text, these are not different cases, they are just alternate ways of looking at the same thing. More formally, they are alternate ways of arranging the mathematic of the same situation, depending upon the reference population (or economic neighborhood; (78)) with which relatedness is calculated relative to (79, 80). The distinction between Hamiltonian and Wilsonian spite does not appear to have been made by Wilson (75) – his figure showing the indirect benefit to relatives was used to illustrate Hamilton’s idea of spite.

Negative relatedness and spiteful behavior

In this section we provide a more detailed discussion of “negative relatedness”, and how spiteful behavior directed against negative relations can be favored in the same way as altruism directed towards positive relations (following (81)). Although often phrased as a probability of sharing genes in common, the kin selection coefficient of relatedness is actually a statistical measure that describes the genetic similarity of two individuals relative to the population average (59, 82). If the recipient carries the actor’s genes at a higher frequency than the population as a whole (i.e. individual A in the diagram below), then the two individuals are positively related ($r > 0$). Conversely, if the recipient carries the actor’s genes at a lower frequency than the population as a whole (individual B), then the two individuals are negatively related ($r < 0$). Finally, if the recipient carries the actor’s genes at a frequency that is equal to the population as a whole, then the two individuals are zero related ($r = 0$). It follows that the average relatedness in the population is zero.

Relatedness provides a measure of value, describing how valuable is the reproductive success of one individual relative to the reproductive success of another individual, from the perspective of the latter (83). If an actor and recipient are positively related, then the actor can increase the frequency of its own genes in the population by promoting the reproductive success of the recipient. This is the source of the indirect fitness benefit that drives the evolution of altruistic behaviors (2). Alternatively, if the actor and recipient are negatively related, then the actor can increase the frequency of its own genes in the population by *reducing* the reproductive success of the recipient. This is the source of the indirect fitness benefit that drives the evolution of spiteful behaviors (59). In other words, losing a negative relation is equivalent to gaining a relative! An alternative way of conceptualizing this is that by harming individuals to whom the actor

is not related, this reduces competition faced by the relatives of the actor, and hence is favored as a form of indirect altruism (79, 80).

It can be difficult for organisms to identify which members of their population are, on average, sufficiently negatively related to make costly spiteful behavior worthwhile (77). Kin discrimination and greenbeard mechanisms provide potential solutions. For example, if an individual bearing a greenbeard gene can recognize which other members of its population are carriers and non-carriers, then the proportion p of individuals in the role of carrier have a relatedness of 1, whereas the proportion $1-p$ in the role of non-carriers have relatedness of r . Because the average relatedness in the population is zero, we may write $p \times 1 + (1-p) \times r = 0$ and this can be rearranged to express the relatedness of a non-greenbeard recipient to a greenbeard actor as $r = -p/(1-p)$. This negative relatedness decreases from a maximum of zero in the limit of a vanishingly rare greenbeard ($r \rightarrow 0$ as $p \rightarrow 0$) to negative infinity as the greenbeard approaches fixation ($r \rightarrow -\infty$ as $p \rightarrow 1$).

Greenbeards

In addition to those discussed in the main text, a number of other greenbeards have been found. The cell surface gene *FLO1* in the yeast *Saccharomyces cerevisiae* seems to have very similar effects, leading to cooperative adherence with other cells that contain this gene (84). Another example is the tumour-inducing (Ti) plasmid in the bacterial plant pathogen *Agrobacterium tumefaciens*, which is inserted into plant cells to induce cell division and the synthesis of opines, an energy source that can be exploited only by bacteria carrying the plasmid (85). Finally, the b allele at the *OBV* locus in side-blotched lizards - homozygote (bb) males recognize each other, via their distinctive blue throat coloration, and form cooperative mate-guarding dyads (86). In this case, the phenotypic marker and cooperative behavior are encoded by different loci that are physically separated, but they are held in tight linkage disequilibrium by the strong correlational selection related to their mating system.

It is possible to conceptualize the cytoplasmic incompatibility induced in many insects by bacteria such as *Wolbachia* and *Cardinium* as a spiteful greenbeard, if the presence or absence of bacteria is regarded as different ‘alleles’ (53, 77, 87). The bacteria are transmitted through the host’s eggs but not its sperm, and bacteria present in the testes modify sperm cells so that they give rise to unviable progeny unless the egg fertilized by the modified sperm also carries the infection. A number of theoretical models have examined the spread of cytoplasmic incompatibility and the influence of population structure (88-92), giving results analogous to that in the spite and greenbeard literature (77, 81).

Greenbeard Dynamics

A number of papers have modeled greenbeard effects, although this was not always realized at the time (40, 41, 81, 93-100). These models are reviewed elsewhere (81). The general point in all of these models is that there is some assortment mechanism that ensures the social behavior is preferentially directed at or away from other carriers of that gene (81, 93, 99, 101). A summary of the evolutionary dynamics of greenbeards, and how they differ for the four types of greenbeard are discussed in detail elsewhere (81). The main points are that: (1) selection is positively frequency dependent for all types

except for facultative-helping, with the greenbeard gene disfavored at low frequency and favored at high frequency; (2) when greenbeards are favored, they are selected to go to fixation, which can obscure them. With bacteriocins, there is the added complication that bacteria can evolve costly resistance to bacteriocins, which can set up a balanced polymorphism between producers, resistants and sensitives, reminiscent of the rock-scissors-paper game (102, 103). A key task for the future is to link spite theory to these dynamics, and multiple types of bacteriocin.

Genomic outlaws

It is often assumed that greenbeards are intragenomic outlaws, in conflict with the rest of the genome. However, this is not the case (81). Whilst there is selection at the rest of the genome to suppress the altruistic or spiteful action, while maintaining the signal (i.e. to become a falsebeard), there is exactly the same selection at the greenbeard locus itself. This is because whilst the behavior encoded by a greenbeard gene incurs a direct fitness cost, wearers of greenbeard benefit from the behavior of other greenbeard individuals, so that (on average) carrying a greenbeard gene may improve an individual's fitness. Modifiers at other loci will be favored to suppress the greenbeard mechanism when the benefit of wearing the beard does not outweigh the cost of greenbeard behavior, but in these situations the greenbeard allele is itself disfavoured (selection occurs in the same direction at all loci). Modifiers that suppress the behavior but not the growth of the beard will always be favoured, but so too is a 'falsebeard' allele arising at the greenbeard locus that achieves the same effect (again, selection occurs in the same direction at all loci)

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