

# GREENBEARDS

Andy Gardner<sup>1,2</sup> and Stuart A. West<sup>1</sup>

<sup>1</sup>*Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, United Kingdom*

<sup>2</sup>*E-mail: andy.gardner@zoo.ox.ac.uk*

Received July 15, 2009

Accepted August 25, 2009

Greenbeards are genes that can identify the presence of copies of themselves in other individuals, and cause their bearer to behave nepotistically toward those individuals. In recent years, a number of examples have been discovered, and it has been suggested that greenbeards represent one of the fundamental routes to social behaviors such as cooperation. However, despite their possible theoretical and empirical importance, many basic aspects of greenbeard biology are commonly misunderstood. Here, we distinguish between four different types of greenbeard, which differ in their evolutionary dynamics. We show that all four types exist, and that they differ in the ease with which they can be empirically detected. We clarify the inclusive fitness explanation of greenbeards, and show that they are not intragenomic outlaws. Finally, we argue that although greenbeards are likely to be most common and easiest to detect in microorganisms, they are unlikely to be important in organisms such as humans.

**KEY WORDS:** Altruism, chloropogonology, Hamilton's rule, inclusive fitness, kin selection, relatedness, spite.

## What Are Greenbeards?

Darwin (1859) argued that natural selection favors those individuals that achieve greater reproductive success, and that this process leads organisms to appear designed as if to maximize their fitness relative to other individuals in the breeding population. This idea was formalized by Fisher (1930; Grafen 2002), who fused Darwinism with Mendelism to define fitness in terms of an individual's genetic contribution to future generations (Grafen 2006a). However, this view of self-interested adaptation fails to account for a vast range of social behaviors in the natural world, such as those exhibited by sterile workers in insect colonies, which do not function to maximize the individual's fitness. Explaining such altruistic behavior is a major challenge for evolutionary biologists (Maynard Smith and Szathmari 1995; Hamilton 1996).

Darwin (1859) suggested that worker traits could be favored by natural selection when they provide a benefit to reproductive family members within the colony. More than a century later, Hamilton (1964) developed this insight into the modern theory of inclusive fitness. The ultimate criterion for a gene to be favored by natural selection is if it increases the frequency of copies of itself among future generations. It can achieve this in two ways: first, by improving the fitness of its bearer (direct fitness benefit);

and second, by improving the fitness of other individuals who carry copies of the same gene (indirect fitness benefit). Hence, altruism can be favored provided that the indirect fitness benefit is greater than the direct fitness cost and, more generally, natural selection leads individuals to appear designed as if to maximize their inclusive fitness (Hamilton 1964, 1970; Grafen 2006b).

The usual reason why two individuals would share genes is because they are genealogical relatives, so this process has often been termed "kin selection" (Maynard Smith 1964). However, the theory of inclusive fitness applies whenever social partners share a gene in common, irrespective of the causes of this genetic similarity, and even when they are dissimilar at other loci elsewhere in the genome. Hamilton (1964, pp. 24–25) illustrated this using a thought experiment, in which he imagined a gene (or a cluster or tightly-linked genes) with the following three properties: (1) it gives rise to a conspicuous phenotype; (2) it uses this phenotypic "marker" to discriminate between carriers and noncarriers of the gene; and (3) it leads the individual to behave nepotistically toward other carriers of the gene, at a personal cost to himself. Hamilton showed that such a gene could be favored by natural selection, even if carriers shared no other genes in common. This clarified that the crucial requirement for altruism is genetic

relatedness (rather than genealogical relationship) at the altruism locus (rather than over the whole genome).

In *The Selfish Gene*, Dawkins (1976) used Hamilton's thought experiment to champion this gene's eye view of natural selection more generally. Famously, Dawkins used the example of carrier individuals growing conspicuous green beards, and directing cooperative behavior toward other individuals bearing green beards. Consequently, this mechanism has been termed the "greenbeard effect." More generally, the greenbeard effect does not require the use of a phenotypic marker, but requires that the gene for the social behavior (or a closely linked gene) encodes an assortment mechanism that ensures nepotistic behavior in favor of other carriers of the gene—for example, if a cooperation gene has a pleiotropic effect on habitat preference that leads gene carriers to settle together (Hamilton 1975). The greenbeard effect is one of two basic mechanisms for the evolution of altruistic behavior, the other being interaction with genealogical kin, which can occur via kin discrimination or population viscosity (Hamilton 1964, 1975; Lehmann and Keller 2006; West et al. 2007a).

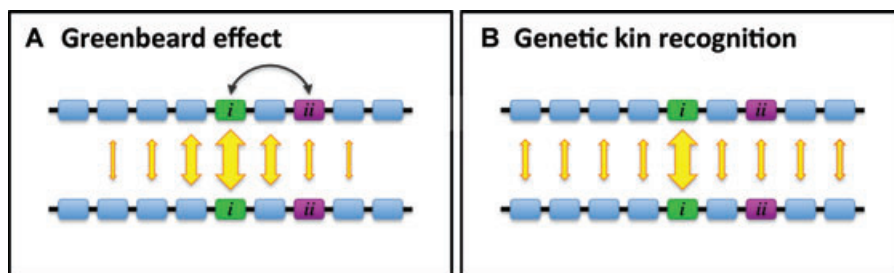
It is useful to distinguish greenbeards from genetic kin recognition (Fig. 1). Dawkins (1982) distinguished greenbeards from a phenotype matching mechanism that he termed the "armpit effect." The latter involves individuals recognizing a phenotypic marker carried both by themselves and by their social partners, and behaving nepotistically on the basis of this phenotypic similarity (Hamilton 1964; Mateo and Johnston 2000; Rousset and Roze 2007; Lehmann et al. 2009). For example, the rule "be kind to neighbours who smell similar to you." Thus, while the greenbeard mechanism operates owing to statistical associations between different loci within individuals (classical linkage disequilibrium; pleiotropy being an extreme form of this), the armpit mechanism operates owing to genealogical kinship. A key difference is that green beards lead to a high relatedness only at the greenbeard locus and closely linked loci (cooperation between nongenealogical relatives), whereas kin recognition methods such as phenotype

matching can lead to a relatively high relatedness over most of the genome (cooperation between genealogical relatives; Grafen 1990). A consequence of this is that cheats that display a green beard, or assorting behavior, without also performing the cooperative behavior ("falsebeards"), could invade and overrun the population (Dawkins 1976; Maynard Smith 1976; Grafen 1984; Pepper and Smuts 2002). For this reason, as well as their supposed complexity, greenbeards have generally been considered to be unimportant in the real world, with more attention being given to the other mechanisms that generate appreciable genetic relatedness between social partners, such as kin recognition and population viscosity.

### Four Kinds of Greenbeard

Dawkins' (1976, 1982) popularization of the greenbeard mechanism neglected the fact that there are four distinct types of greenbeard, which differ in their evolutionary dynamics and likelihood of being observed (Table 1, Misconception 1; Fig. 2). First, greenbeards could involve the actor helping a fellow greenbeard social partner, as in Dawkins' account, or alternatively they could involve the actor harming a nongreenbeard social partner. So, we distinguish "helping" and "harming" greenbeards (Gardner and West 2004). Second, discrimination could occur by the actor adjusting his behavior in response to the beard status of his social partners, or alternatively by the actor performing a fixed behavior, which affects recipients differently, depending upon whether they carry the greenbeard gene. So, we also distinguish "facultative" and "obligate" greenbeards (Queller 1984). The four possibilities defined by this  $2 \times 2$  classification are outlined in Figure 2.

Contrary to the initial prediction that greenbeards would not exist in nature, each of the four hypothetical types is represented by at least one real-world example (Fig. 3). The classic facultative-helping type of greenbeard is illustrated by cell adhesion in *Dictyostelium discoideum* (Queller et al. 2003; Fig. 3A).



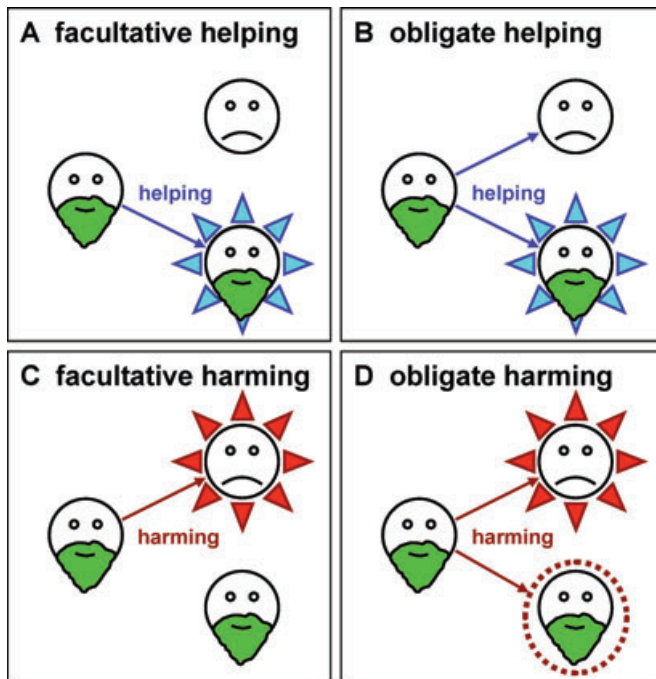
**Figure 1.** Greenbeard effect versus genetic kin recognition. (A) The greenbeard effect is mediated by linkage disequilibrium (black arrow) between beard (i) and behavior (ii) loci. Fellow beard bearers (the two individuals whose genomes are shown in alignment) are strongly related ( $r = 1$ , thick yellow arrow) at the beard locus and hence also related (yellow arrows) at other loci that are in linkage disequilibrium with the beard locus—possibly including genes for social behavior. (B) Genetic kin recognition is mediated by genealogical relatedness between social partners. Individuals sharing a phenotypic marker—and hence a marker gene (i)—in common are more likely to be close kin, and hence genetically similar ( $r > 0$ ) at all loci across the genome—including genes for social behavior (ii).

**Table 1.** Five misconceptions regarding the greenbeard effect.

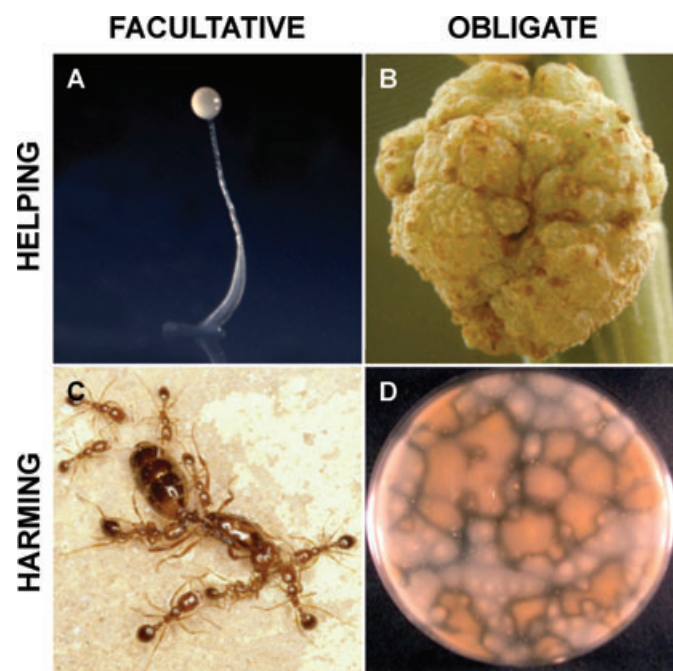
Misconception	Reality
1 There is one type of greenbeard (facultative helping)	There are four distinct types of greenbeard (helping vs. harming, facultative vs. obligate)
2 Greenbeard evolution is not captured by Hamilton's rule	Greenbeard evolution is captured by Hamilton's rule
3 Greenbeard genes are intragenomic outlaws	Selection at other loci operates identically with selection at the greenbeard locus
4 The greenbeard effect is a type of genetic kin recognition	The greenbeard effect is distinct from genetic kin recognition (armpit effect)
5 The greenbeard effect provides a robust explanation for cooperation in organisms such as humans and social insects	The greenbeard effect is often vulnerable to "falsebeard" cheating, and so is unlikely to be important in organisms such as humans or social insects

Individuals with the *csa* gene adhere to each other in aggregation streams, and form cooperative fruiting bodies, whereas noncarriers of the gene are excluded from these social groups. 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 (Smukalla et al. 2008). These examples support Haig's (1996) insight that cell adhesion genes—which can mediate both self-recognition and social interaction functions—could provide real-world examples



**Figure 2.** There are four types of greenbeard. (A) Facultative-helping greenbeards, such as those described by Dawkins (1976, 1982), involve the greenbeard actor facultatively adjusting his social behavior so as to provide help only to those social partners who also carry the greenbeard gene. (B) Obligate-helping greenbeards involve the actor expressing the helping behavior in all social interactions, but only carriers of the greenbeard gene can benefit from this help. (C) Facultative-harming greenbeards involve the actor facultatively adjusting his social behavior so as to inflict harm only against those social partners who do not carry the greenbeard gene. (D) Obligate-harming greenbeards involve the actor expressing the harming behavior in all social interactions, but carriers of the greenbeard gene are immune to the behavior's harmful effects.



**Figure 3.** Greenbeards in the real world. (A) Facultative-helping greenbeards include the *csa* cell adhesion gene in the social amoeba *Dictyostelium discoideum*, which forms cooperative fruiting bodies (Photo credit: O. Gilbert). (B) Obligate-helping greenbeards include the Ti (tumor-inducing) plasmid of the bacterium *Agrobacterium tumefaciens*, responsible for gall formation in plants (Photo credit: H. Aarnes). (C) Facultative-harming greenbeards include the *Gp-9* gene of the red fire ant *Solenopsis invicta*, which makes carrier workers execute noncarrier queens (Photo credit: J. All & K. Ross). (D) Obligate-harming greenbeards include bacteriocin-encoding genes of the bacterium *Photorhabdus luminescens*, responsible for the inhibition zones (bacterial No Man's Land) on this agar plate (Photo credit: R. Massey).

of greenbeard mechanisms (Summers and Crespi 2005; Burt and Trivers 2006). A further example of a facultative-helping greenbeard is provided by the *b* allele at the *OBV* locus in side-blotched lizards (Sinervo and Clobert 2003). Here, homozygote (*bb*) males recognize each other, via their distinctive blue throat coloration, and form cooperative mate-guarding dyads. Although the phenotypic marker and cooperative behavior are encoded by different loci that are physically separated, they are held in tight linkage disequilibrium, owing to strong correlational selection related to their mating system.

An example of an obligate helping greenbeard is provided by the tumour-inducing (Ti) plasmid in the bacterial plant pathogen *Agrobacterium tumefaciens* (White and Winans 2007; Fig. 3B). In this species, the plasmid is inserted into plant cells, where it induces cell division and the synthesis of opines, an energy source that can be exploited only by bacteria carrying the plasmid. Interestingly, Dawkins (1982) described the biology of this example only a few pages after stating that greenbeards would not exist in nature, apparently overlooking the plasmid's relevance to greenbeard theory.

Turning to harming greenbeards, an example of a facultative-harming greenbeard is provided by the *Gp-9* gene of the fire ant, *Solenopsis invicta* (Keller and Ross 1998; Ross and Keller 2002; Fig. 3C). Workers with the *b* allele at this locus use odor to determine whether prospective queens also carry this allele—and decapitate them if they do not. An example of obligate-harming greenbeards is provided by bacteriocin-encoding genes, which are present in all major bacterial lineages (Riley and Wertz 2002; Fig. 3D). Bacteriocins are toxins that have a narrow range of antimicrobial action, often limited to members of the same species as the producer cell (Riley et al. 2003). Immunity to the toxin is conferred upon clonemates of the producer cell, owing to tight linkage between the bacteriocin-encoding gene and a gene encoding a factor that deactivates the bacteriocin (Riley and Wertz 2002). Another example of obligate harming is the cytoplasmic incompatibility induced in many insects by bacteria such as *Wolbachia* (Werren 1997) and *Cardinium* (Hunter et al. 2003). 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 inviable progeny unless the egg fertilized by the modified sperm also carries the infection. This can be considered a greenbeard mechanism if the presence or absence of bacteria is regarded as different host "alleles."

## Greenbeard Evolution

Hamilton's (1964, 1970) rule states that any trait is favored by natural selection provided that  $rB - C > 0$ , where  $C$  is the fitness cost to the actor,  $B$  is the fitness benefit to the recipient, and  $r$  is the coefficient of genetic relatedness between actor and recipient,

with respect to the gene(s) underlying the trait. Hamilton's rule represents a simple encapsulation of the direct ( $-C$ ) and indirect ( $rB$ ) fitness consequences of a trait, and the sum of these two terms is the total inclusive fitness effect. Social behaviors are defined according to their fitness impact upon actor and recipient, as: altruism ( $B > 0$ ,  $C > 0$ ); mutual benefit ( $B > 0$ ,  $C < 0$ ); selfishness ( $B < 0$ ,  $C < 0$ ); and spite ( $B < 0$ ,  $C > 0$ ) (Hamilton 1964; West et al. 2007b). Here, we use Hamilton's rule to understand how greenbeard genes can be favored by natural selection in a large, well-mixed population, and to classify them according to Hamilton's scheme. The same results can alternatively be derived using a more formal population genetics approach (see Appendix for details). For simplicity, we consider a single locus with two (greenbeard and nongreenbeard) alleles. However, the possibility for multiple, cosegregating greenbeard alleles presents an interesting problem for future study.

Helping greenbeards are altruistic and favored owing to indirect fitness benefits ( $rB > 0$ ; Table 2). Individuals bearing facultative-helping greenbeards incur a fitness cost  $c$  owing to their helping behavior, but only in encounters with fellow greenbeards. Hence, the net direct fitness cost is  $C = pc$ , where  $p$  is the population frequency of greenbeard individuals. The individual also provides a benefit  $b$  to their social partners, but only in encounters with fellow greenbeards, and so the relatedness at the greenbeard locus conditional upon the benefit being received is  $r = 1$ . Hence, the net indirect fitness benefit is  $rB = pb$ . Thus, the total inclusive fitness effect is  $rB - C = p(b - c)$ , so facultative helping greenbeards are favored if  $b/c > 1$ , i.e., if the benefit to the recipient outweighs the cost to the actor.

Individuals bearing obligate-helping greenbeards incur a fitness cost  $c$  in all encounters, with fellow greenbeards and nongreenbeards alike. Hence, the direct fitness cost for this type of greenbeard is  $C = c$ . Again, the individual provides a benefit  $b$  to their social partners only in encounters with fellow greenbeards, where relatedness is given by  $r = 1$ . Hence, the indirect fitness benefit is  $rB = pb$ . The total inclusive fitness effect is therefore  $rB - C = pb - c$ , and so obligate-helping greenbeards are favored if  $b/c > 1/p$ , i.e., where the ratio of benefit to cost exceeds the reciprocal of the greenbeard's frequency in the population. Facultative-helping greenbeards evolve more readily than obligate-helping greenbeards, because the latter type pays the extra cost of helping in encounters with nongreenbeard social partners. Because  $B > 0$  and  $C > 0$  for both facultative and obligate types, the behavior encoded by helping greenbeard genes is altruistic (Hamilton 1964; West et al. 2007b).

Harming greenbeards are spiteful traits that are favored owing to indirect fitness benefits ( $rB > 0$ ; Table 2). Because the behavior is costly to the recipient ( $B < 0$ ), this requires that there be a negative relatedness between actor and recipient ( $r < 0$ ) at the greenbeard locus (Hamilton 1970; Grafen 1985). Genetic



**Table 2.** Greenbeard genes are favored owing to indirect fitness benefits

Greenbeard type	Fitness cost for actor, $C$	Fitness benefit for recipient, $B$	Genetic relatedness, $r$	Condition to be favored
Helping, facultative	$pc$	$pb$	1	$\frac{b}{c} > 1$
Helping, obligate	$c$	$pb$	1	$\frac{b}{c} > \frac{1}{p}$
Harming, facultative	$(1-p)a$	$-(1-p)d$	$-\frac{p}{1-p}$	$\frac{d}{a} > \frac{1-p}{p}$
Harming, obligate	$a$	$-(1-p)d$	$-\frac{p}{1-p}$	$\frac{d}{a} > \frac{1}{p}$

The components of inclusive fitness are the fitness cost to the actor ( $C$ ), the fitness benefit to the recipient ( $B$ ), and the genetic relatedness of actor and recipient ( $r$ ). In particular, inclusive fitness is the sum of the direct fitness effect ( $-C$ ) and the indirect fitness effect ( $rB$ ), and the greenbeard is favored by natural selection when  $rB - C > 0$ . These calculations assume an infinite, well-mixed population. Other parameters:  $a$ , the cost of harming;  $b$ , the benefit of receiving help;  $c$ , the cost of helping;  $d$ , the cost of receiving harm;  $p$ , the frequency of greenbeards in the population.

relatedness is a statistical concept, and negative relatedness simply means that two individuals are genetically less similar than average (see Box 1). Individuals bearing a facultative-harming greenbeards pay a fitness cost  $a$  only in encounters with nongreenbeard social partners, and hence incur a net direct fitness cost of  $C = (1-p)a$ , where  $1-p$  is the frequency of nongreenbeard individuals in the population. Such greenbeard individuals also inflict a fitness decrement  $d$  against nongreenbeard social partners, and hence  $B = -(1-p)d$ . They are negatively related to the victims of their harming behavior, by  $r = -p/(1-p)$  (Box 1), hence the total inclusive fitness effect is  $rB - C = pd - (1-p)a$ , and so facultative-harming greenbeards are favored if  $d/a > (1-p)/p$ , i.e., where the ratio of harm inflicted to cost incurred is greater than the ratio of nongreenbeard to greenbeard individuals in the population.

Individuals bearing an obligate-harming greenbeard pay a fitness cost  $a$  in all encounters, with greenbeard and nongreenbeard social partners alike, giving a net direct fitness cost of  $C = a$ . And they inflict a fitness decrement  $d$  against nongreenbeard social partners—i.e.,  $B = -(1-p)d$ —to whom they are related by  $r = -p/(1-p)$ . Hence, the total inclusive fitness effect is  $rB - C = pd - a$ , and so obligate-harming greenbeards are favored if  $d/a > 1/p$ , i.e., where the ratio of harm inflicted to cost incurred is greater than the reciprocal of the greenbeard's frequency in the population. As with helping greenbeards, facultative-harming greenbeards are more readily favored than obligate-harming greenbeards, because the latter type pays the extra cost of harming even in encounters with fellow greenbeard social partners. Because  $B < 0$  and  $C > 0$  for both facultative and obligate scenarios, the behavior encoded by harming greenbeards is spiteful (Hamilton 1970; Gardner and West 2004).

Queller (1984) suggested that greenbeards involve “synergistic” selection, and that they are not captured by Hamilton's rule,

$rB - C > 0$  (Table 1, Misconception 2). This is because Queller (1984) calculated relatedness as an average over all social partners, irrespective of how they interact. Because greenbeard effects occur even in fully mixed populations, in which this relatedness is zero, Queller (1984) suggested that an altogether different type of selective advantage is involved. However, the appropriate coefficient of relatedness is the average relatedness between actor and recipient, conditional on the latter receiving the social behavior (Hamilton 1964; Dawkins 1976). This leads to a nonzero relatedness, positive ( $r = 1$ ) in the case of helping greenbeards and negative ( $r = -p/(1-p)$ ) in the case of harming greenbeards, and this allows the selective costs and benefits of greenbeards to be fully accounted for using a Hamilton's rule approach (as shown above). (Note that Queller (1985) later added a “correction” factor to Hamilton's rule, so as to capture the greenbeard effect, and other synergistic selection more generally. However, this correction factor is not required to capture the greenbeard effect (as shown by the above analysis), nor is it required to capture synergistic effects more generally (Gardner et al. 2007b, pp. 218–219).)

## Greenbeard Dynamics

The four kinds of greenbeards differ in their evolutionary dynamics. Above, we found that for facultative-helping greenbeards—which have received the most attention in the development of greenbeard theory—the direction of selection is independent of their frequency in the population (Fig. 4A). If the greenbeard is favored when rare, it will increase in frequency and continue to be favored until it is driven to fixation. In contrast, each of the other three types of greenbeard gene are selectively disfavored when at low frequency and selectively favored when at high frequency (positive frequency dependence; Figs. 4B,D). The connection between greenbeard genes and frequency-dependent selection has

## Box 1—Negative relatedness and spiteful behavior

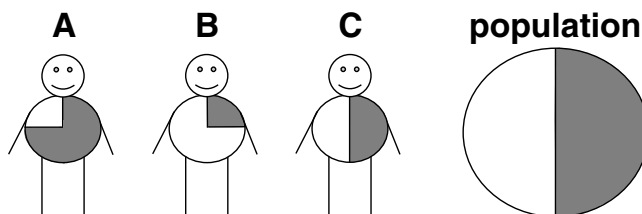
“When a schlemiel leaves the room, you feel as if someone came in.” Leo Rosten

Here, we introduce the concept of “negative relatedness,” and explain how spiteful behavior directed against negative relations can be favored in the same way as altruism directed toward positive relations. 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 (Hamilton 1970; Grafen 1985). 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 (Frank 1998). 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 (Hamilton 1964). 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 (Hamilton 1970). 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 spite is favored as a form of indirect altruism (Lehmann et al. 2006; Gardner et al. 2007a).

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 (Gardner and West 2004). The greenbeard mechanism provides a solution. If an individual bearing a greenbeard gene can recognize which other members of its population are carriers and noncarriers, 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 noncarriers 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 nongreenbeard 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  $p \rightarrow 1$ ).

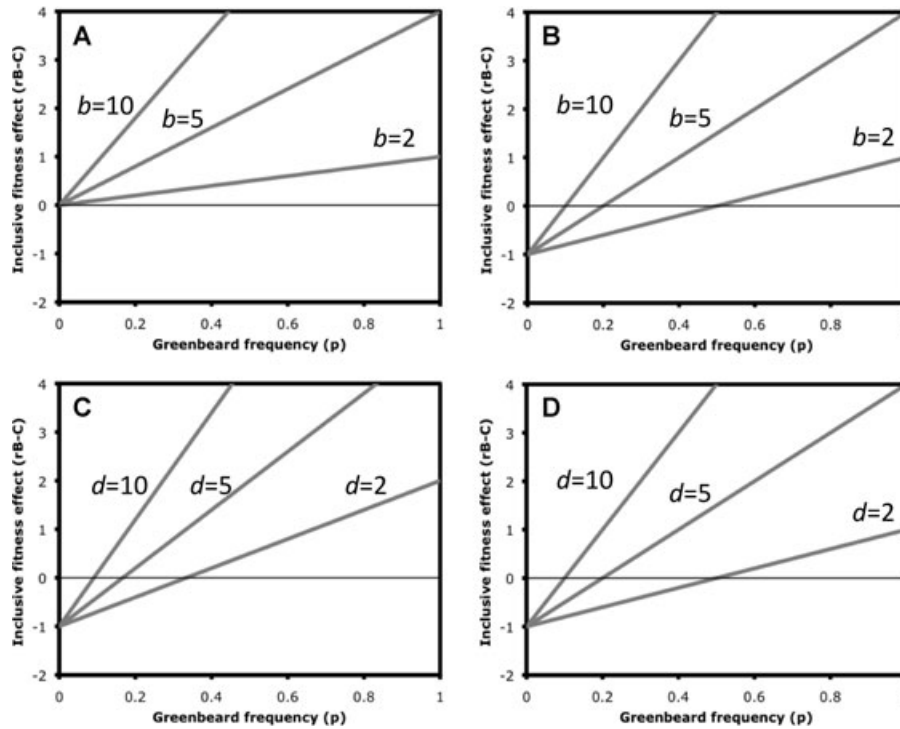


been noted by Queller (1984), who suggested that many kinds of frequency-dependent selection could be reinterpreted as greenbeard effects. This raises the question of how greenbeard genes that are not of the facultative helping type can become established in a population in the first place. In other words, why are they not weeded out by selection as soon as they arise?

One solution to the problem of how greenbeards can become established is if populations are not fully mixed (viscous population). In this case, the local frequency of a greenbeard gene may be high even if its global frequency is vanishingly low. Gardner and West (2004) suggested that if greenbeards are sufficiently frequent—and hence sufficiently favored—within those

localities in which they occur, then they may be able to invade from rarity within the much larger global population. In the simplest scenario of an infinite island model (Wright 1931), we find that population viscosity does indeed promote greenbeard evolution, making it possible for greenbeard genes to invade from rarity (Table 3; see Appendix for details). The role for population structure in promoting the evolution of cytoplasmic incompatibility has been noted by Turelli and Hoffmann (1991; see also Frank 1997).

A potential complication with detecting greenbeards in nature is that, if they can invade, then selection will drive them to fixation, which can obscure the greenbeard mechanism (Fig. 5). For

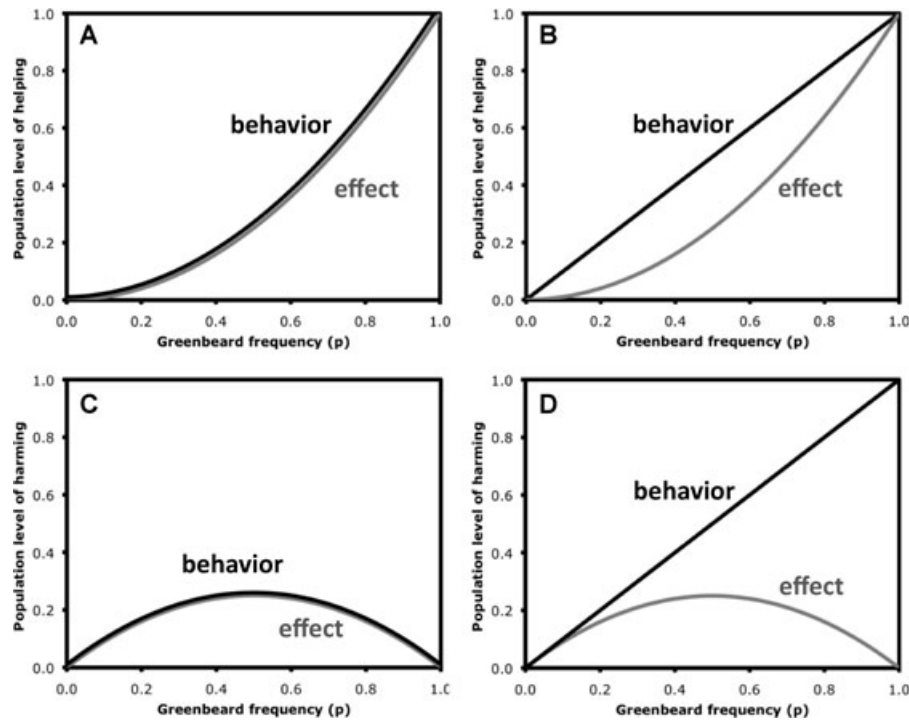


**Figure 4.** Greenbeards and frequency-dependent selection. The inclusive fitness effect of greenbeard behavior is shown across the range of gene frequencies  $0 < p < 1$ : (A) facultative-helping greenbeards are favored at all frequencies ( $b = 2, 5$ , and  $10$ , and  $c = 1$ ); (B) obligate-helping greenbeards are disfavored at low frequency and favored at high frequency ( $b = 2, 5$ , and  $10$ , and  $c = 1$ ); (C) facultative-harming greenbeards are disfavored at low frequency and favored at high frequency ( $d = 2, 5$  and  $10$ , and  $a = 1$ ); (D) obligate-harming greenbeards are disfavored at low frequency and favored at high frequency ( $d = 2, 5$  and  $10$ , and  $a = 1$ ).

**Table 3.** Population structure promotes greenbeard evolution

Greenbeard type	Invasion condition	
	Exact	Approximation
Helping, facultative	$\frac{b}{c} > 1$	$\frac{b}{c} > 1$
Helping, obligate	$\frac{b}{c} > \frac{n-1}{n} \frac{1-(1-m)^2 r_p}{(1-m)^2 (r_p/n - s_p) + (r_p - 1/n)}$	$\frac{b}{c} > 2 + 2M$
Harming, facultative	$\frac{d}{a} > \frac{1-r_p}{(1-m)^2 (r_p - s_p)} - 1$	$\frac{d}{a} > 1 + 2M$
Harming, obligate	$\frac{d}{a} > \frac{n-1}{n} \frac{1-(1-m)^2 r_p}{(1-m)^2 (r_p - s_p)}$	$\frac{d}{a} > 2 + 2M$

We assume the simplest model of population structure—Wright’s (1931) infinite “island” model, in which the population is subdivided into patches of  $n$  individuals, between which there is migration at rate  $m$  per individual per generation (and hence an average of  $M = mn$  migrants per patch per generation)—and that social behavior within patches mediates individual fecundity. Column 2 lists exact invasion conditions for each type of greenbeard, calculated in the limit of weak selection. These depend on the within-patch relatedness coefficient,  $r_p = 1/(n-(n-1)(1-m)^2)$ , and clustering coefficient,  $s_p = (n+2(n-1)(1-m)^2)/((n-(n-1)(1-m)^2)(n^2-(n-1)(n-2)(1-m)^3))$ . Column 3 expresses these invasion conditions in the limit of large patch size and low migration rate (i.e.,  $n \gg 1$ ,  $m \ll 1$ , and  $M$  on the order of 1). Note that indiscriminate helping or harming is not promoted by population viscosity in this model (Taylor 1992; El Mouden and Gardner 2008), so the evolution of helping and harming is due to the greenbeard mechanism and not because population viscosity is favoring helping or harming per se. (See Appendix for details.)



**Figure 5.** Fixation obscures the greenbeard effect. (A) Facultative-helping greenbeards continue to express their helping behavior, and this continues to benefit fellow greenbeards, as the gene progresses to fixation. However, at fixation the helping appears indiscriminate, and hence may be difficult to identify as part of a greenbeard mechanism. (B) Obligate-helping greenbeards continue to express their helping behavior, and this continues to benefit fellow greenbeards, as the gene progresses to fixation. However, at fixation the helping appears indiscriminate, and hence may be difficult to identify as part of a greenbeard mechanism. (C) Facultative-harming greenbeards no longer express their harming behavior as they progress to fixation, owing to the disappearance of nongreenbeard social partners, hence their phenotypic effects disappear in the long term. (D) Obligate-harming greenbeards continue to express their harming behavior as they progress to fixation, but in the absence of nongreenbeard victims, this behavior has no effect and hence may not be identified as greenbeard behavior.

helping greenbeards, the discrimination of greenbeard versus nongreenbeard will not be apparent to the observer, because nongreenbeard individuals will be rare or entirely absent (Haig 1996). However, the helping behaviors will continue to be exhibited, and will continue to have their beneficial effects (Fig. 5A, B). For obligate-harming greenbeards, the harming action will continue to be expressed even in the absence of nongreenbeard victims. However, as this will never be seen to do any harming, it would not be immediately apparent that this was harming behavior (Fig. 5D). In contrast, for facultative-harming greenbeards, once the gene has been driven to fixation there are no nongreenbeard individuals to elicit the harming behavior or to be harmed by this, so that phenotypic effects of the greenbeard gene disappear entirely (Fig. 5C).

Given the above predictions, how have we been able to observe harming greenbeards? Observation of the harming greenbeard effect *Gp-9* gene of the fire ant has been made possible because it has the additional quirk of being lethal in homozygous form (Keller and Ross 1998). The resulting balancing selection ensures the maintenance of both carriers and noncarriers in the population (see also Burt and Trivers 2006; Helantera

2006). Similarly, the persistence of the harming effect of bacteriocins may be due to the possibility for bacteria to evolve costly resistance to bacteriocins, which can set up a balanced polymorphism between producers, resistants and sensitives, reminiscent of the rock-scissors-paper game (Maynard Smith 1982; Kerr et al. 2002; Kirkup and Riley 2004). Polymorphism of different greenbeard alleles has also been observed (Smukalla et al. 2008; K. Foster, pers comm), although the causes of such polymorphism are obscure, and warrant further study. Finally, the phenotypic effects of cytoplasmic incompatibility may persist in the long term owing to imperfect vertical transmission of bacteria, which generates uninfected hosts in every generation (Werren 1997).

### Are Greenbeards Outlaws?

Greenbeard genes are often described as being in conflict with the rest of the genome—i.e., intragenomic outlaws (Alexander and Borgia 1978; Dawkins 1982; Okasha 2002; Helantera and Bargum 2007; Table 1, Misconception 3). However, selection



operating upon modifier alleles at other loci is in the same direction as that operating upon mutant alleles arising at the greenbeard locus, giving a unity across the genome with regard to the greenbeard effect. (Responses to selection may, of course, be quite different between loci, owing to differences in available genetic variation.) This can be shown using a thought experiment, in which we consider the fate of a modifier gene that suppresses the greenbeard mechanism. In applications of modifier theory, it is standard to begin with a population that is at an evolutionary equilibrium. First, we start by assuming that a greenbeard gene has gone to fixation, and we introduce a modifier gene at some other locus that suppresses both the beard (phenotypic marker) and the behavior of the greenbeard gene. Because the original greenbeard gene is fixed, the modifier locus is the sole determinant of whether the individual expresses the greenbeard phenotype or the nonbeard phenotype. Hence, it effectively becomes the greenbeard locus, and an analysis of selection operating at this locus exactly recovers the results presented in Table 3. In other words, there is no interlocus conflict over the decision to express or suppress the greenbeard mechanism (Ridley and Grafen 1981; Dawkins 1982; Okasha 2002).

Second, we consider a population in which the greenbeard gene has gone to fixation, and we introduce a modifier gene at an unlinked locus that suppresses the greenbeard behavior without suppressing the growth of the beard. This could involve either a decoupling of pleiotropic effects within a single individual or else, in systems in which actor and recipients roles are fulfilled by different classes (such as *Gp-9* in the fire ant, where the behavior is enacted by workers and the marker is exhibited by prospective queens; Keller and Ross 1998), by suppressing the expression of the gene in the actor class only. This means that the modifier locus is the sole determinant of the greenbeard phenotype, with carriers of the modifier gene expressing a falsebeard and with carriers of the null allele at the modifier locus expressing the usual greenbeard phenotype. Here, the falsebeard is selectively favored at all frequencies (see Appendix for details), hence if it is possible to decouple the beard and behavior effects of greenbeard genes, then modifiers at other loci will be favored to do this (Ridley and Grafen 1981; Hamilton 1987; Okasha 2002; Grafen 2006b; Helanterä and Bargum 2007). However, this selective advantage equally applies to falsebeard alleles arising at the original greenbeard locus, either by mutation or recombination (Lehmann and Keller 2006). In other words, there is no interlocus conflict over the decision to express or suppress the greenbeard's social behavior—selection operates in the same way at all loci involved.

## Confusing Beards

Much confusion in the literature on the evolution of cooperation has stemmed from a failure to understand the greenbeard

effect. First, the term greenbeard is sometimes used to refer to scenarios where the beard and behavior are not performed by the same gene or closely linked genes (Jansen and van Baalen 2006; Nowak 2006; Table 1, Misconception 4). However, this is simply kin recognition (the armpit effect), and does not satisfy the proper definition of the greenbeard mechanism (Hamilton 1964; Dawkins 1982; Rousset and Roze 2007). This difference is important because greenbeards have different dynamics, are likely to differ in their importance, and because a failure to distinguish mechanisms obscures the relationship between these models and the more general literature on kin recognition (Rousset and Roze 2007). For example, Jansen and van Baalen (2006) suggest that their results “imply that the scope for green beard genes is much wider than often assumed,” whereas really they are showing that mutation pressure can solve Crozier's paradox, which is an interesting—but altogether different—problem concerning the tendency for kin recognition mechanisms to erode the diversity of those genetic markers upon which they are dependent (Crozier 1986; Grafen 1990; Rousset and Roze 2007).

Second, some models for cooperation implicitly invoke greenbeard mechanisms, without this having been realized or stated (Eshel and Cavalli-Sforza 1982; Frank 1987; Wilson and Dugatkin 1997; Gintis 2000; Owren and Bachorowski 2001; Avilés 2002; Bowles and Gintis 2004; Seabright 2004; Wilson and Hölldobler 2005; Table 1, Misconception 5). This is usually done in situations in which there is no reason to suspect that the marker and cooperative behavior are encoded by the same gene or closely linked genes, or that falsebeards could not arise, and so the proposed explanation for cooperation would not be evolutionarily stable. This error occurs in several models that have been proposed to explain cooperation in humans, including the idea that individuals who cooperate differ from individuals who cheat in “some observable characteristic” (Frank 1987), such as being more likely to smile and laugh (Owren and Bachorowski 2001; Seabright 2004). Another example from the literature on human cooperation is provided by some (but not all) models of “strong reciprocity” in which cooperation and punishment are assumed to be completely linked traits (Gintis 2000; Bowles and Gintis 2004). Here, cooperation acts as a phenotypic marker indicating that the individual is also a punisher, and hence punishment of noncooperators is favored as a facultative-harming greenbeard trait (Lehmann et al. 2007). Finally, Wilson and Hölldobler (2005) have recently suggested that eusociality in insects evolved as a consequence of individuals with altruistic alleles settling together, irrespective of their genealogical closeness. However, this argument is prone to the usual problems associated with greenbeards, and phylogenetic data support the more standard explanation of indirect benefits through helping genealogical relatives (Boomsma 2007; Helanterä and Bargum 2007; Hughes et al. 2008).

## Conclusions

To conclude, how common are greenbeards likely to be, and where are we most likely to find them? Greenbeards were initially conceived as a thought experiment to illustrate a technical point about genetic relatedness, and were thought unlikely to occur in the real world (Hamilton 1964; Dawkins 1976; Maynard Smith 1976; Dawkins 1982; Grafen 1984). However, as discussed above, a number of examples have been found in recent years, spanning all four different types of greenbeard (Fig. 2). Furthermore, although theory suggests that greenbeards will be rare, we have also shown that greenbeards would often be hard to find, because frequency-dependent selection would usually drive them to fixation (Fig. 4), making their effects difficult to detect (Fig. 5). It is also perhaps no coincidence that most examples of greenbeards come from microorganisms. Here, the relatively simpler link between genotype and phenotype may prevent a decoupling of beard and behavior, and hence prohibit the evolution of falsebeards that display the beard but not the behavior. In addition, it may also be easier to empirically detect greenbeards in microorganisms, where genetic knockouts are routinely used, resolving the difficulty of observing greenbeards once they have reached fixation. Consequently, the recent growth in the study of greenbeards (chloropogonology) may be a byproduct of the growing interest in the social behavior of microbes (West et al. 2006; Foster et al. 2007).

## ACKNOWLEDGMENTS

We thank H. Aarnes, O. Gilbert, R. Massey, and K. Ross for images, N. Barton, K. Foster, H. Helanterä, and D. Queller for discussion, and the European Research Council and the Royal Society for funding.

## LITERATURE CITED

- Alexander, R. D., and G. Borgia. 1978. Group selection, altruism, and levels of organization of life. *Annu. Rev. Ecol. Evol. Syst.* 9:449–474.
- Avilés, L. 2002. Solving the freeloader's paradox: genetic associations and frequency-dependent selection in the evolution of cooperation among nonrelatives. *Proc. Natl. Acad. Sci. USA* 99:14268–14273.
- Boomsma, J. J. 2007. Kin selection versus sexual selection: why the ends do not meet. *Curr. Biol.* 17:R673–R683.
- Bowles, S., and H. Gintis. 2004. The evolution of strong reciprocity: cooperation in heterogeneous populations. *Theor. Popul. Biol.* 65:17–28.
- Burt, A., and R. Trivers. 2006. *Genes in conflict: the biology of selfish genetic elements*. Harvard Univ. Press, Cambridge, MA.
- Crozier, R. H. 1986. Genetic clonal recognition abilities in marine invertebrates must be maintained by selection for something else. *Evolution* 40:1100–1101.
- Darwin, C. 1859. *On the origin of species by means of natural selection, or, the preservation of favoured races in the struggle for life*. John Murray, London, UK.
- Dawkins, R. 1976. *The selfish gene*. Oxford Univ. Press, Oxford.
- . 1982. *The extended phenotype*. Oxford Univ. Press, Oxford.
- El Mouden, C., and A. Gardner. 2008. Nice natives and mean migrants: the evolution of dispersal-dependant social behaviour in viscous populations. *J. Evol. Biol.* 21:1480–1491.
- Eshel, I., and L. L. Cavalli-Sforza. 1982. Assortment of encounters and evolution of cooperativeness. *Proc. Natl. Acad. Sci. USA* 79:1331–1335.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. Clarendon, Oxford.
- Foster, K. R., K. Parkinson, and C. R. L. Thompson. 2007. What can microbial genetics teach sociobiology? *Trends. Genet.* 23:73–80.
- Frank, R. H. 1987. If *Homo Economicus* could choose his own utility function, would he want one with a conscience? *Am. Econ. Rev.* 77:593–604.
- Frank, S. A. 1997. Cytoplasmic incompatibility and population structure. *J. Theor. Biol.* 184:327–330.
- . 1998. *Foundations of social evolution*. Princeton Univ. Press, Princeton, NJ.
- Gardner, A., I. C. W. Hardy, P. D. Taylor, and S. A. West. 2007a. Spiteful soldiers and sex ratio conflict in polyembryonic parasitoid wasps. *Am. Nat.* 169:519–533.
- Gardner, A., S. A. West, and N. H. Barton. 2007b. The relation between multilocus population genetics and social evolution theory. *Am. Nat.* 169:207–226.
- Gardner, A., and S. A. West. 2004. Spite and the scale of competition. *J. Evol. Biol.* 17:1195–1203.
- . 2006. Demography, altruism, and the benefits of budding. *J. Evol. Biol.* 19:1707–1716.
- Gintis, H. 2000. Strong reciprocity and human sociality. *J. Theor. Biol.* 206:169–179.
- Grafen, A. 1984. Natural selection, kin selection and group selection. Pp. 62–84 in J. R. Krebs and N. B. Davies, eds. *Behavioural ecology: an evolutionary approach*. Blackwell Scientific Publications, Oxford, UK.
- . 1985. A geometric view of relatedness. *Oxford Surv. Evol. Biol.* 2:28–89.
- . 1990. Do animals really recognise kin? *Anim. Behav.* 39:42–54.
- . 2002. A first formal link between the Price equation and an optimization program. *J. Theor. Biol.* 217:75–91.
- . 2006a. A theory of Fisher's reproductive value. *J. Math. Biol.* 53:15–60.
- . 2006b. Optimisation of inclusive fitness. *J. Theor. Biol.* 238:541–563.
- Haig, D. 1996. Gestational drive and the green-bearded placenta. *Proc. Natl. Acad. Sci. USA* 93:6547–6551.
- Hamilton, W. D. 1964. The genetical evolution of social behaviour, I & II. *J. Theor. Biol.* 7:1–52.
- . 1970. Selfish and spiteful behaviour in an evolutionary model. *Nature* 228:1218–1220.
- . 1971. Selection of selfish and altruistic behaviour in some extreme models. Pp. 57–91 in J. F. Eisenberg, and W. S. Dillon, eds. *Man and beast: comparative social behavior*. Smithsonian Press, Washington, DC.
- . 1975. Innate social aptitudes of man: an approach from evolutionary genetics. Pp. 133–155 in R. Fox, ed. *Biosocial anthropology*. Wiley, New York.
- . 1987. Discriminating nepotism: expectable, common, overlooked. Pp. 417–437 in D. J. C. Fletcher and C. D. Michener, eds. *Kin recognition in animals*. Wiley, New York.
- . 1996. *Narrow roads of gene land: I evolution of social behaviour*. W.H. Freeman, Oxford.
- Helanterä, H. 2006. The unity that does not exist—a review of A. Burt & R. Trivers 2006: genes in conflict. *J. Evol. Biol.* 19:2067–2070.
- Helanterä, H., and K. Bargum. 2007. Pedigree relatedness, not greenbeard genes, explains eusociality. *Oikos* 116:217–220.
- Hughes, W. O. H., B. P. Oldroyd, M. Beekman, and F. L. W. Ratnieks. 2008. Ancestral monogamy shows kin selection is the key to the evolution of eusociality. *Science* 320:1213–1216.
- Hunter, M. S., S. J. Perlman, and S. E. Kelly. 2003. A bacterial symbiont in the *Bacteroides* induces cytoplasmic incompatibility in the

- parasitoid wasp *Encarsia pergandiella*. Proc. R. Soc. Lond. B 270:2185–2190.
- Jansen, V. A. A., and M. van Baalen. 2006. Altruism through beard chromodynamics. Nature 440:663–666.
- Keller, L., and K. G. Ross. 1998. Selfish genes: a green beard in the red fire ant. Nature 394:573–575.
- Kerr, B., M. A. Riley, M. W. Feldman, and J. M. Bohannan. 2002. Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. Nature 418:171–174.
- Kirkup, B. C., and M. A. Riley. 2004. Antibiotic-mediated antagonism leads to a bacterial game of rock-paper-scissors in vivo. Nature 428:412–414.
- Lehmann, L., and L. Keller. 2006. The evolution of cooperation and altruism. A general framework and classification of models. J. Evol. Biol. 19:1365–1378.
- Lehmann, L., K. Bargum, and M. Reuter. 2006. An evolutionary analysis of the relationship between spite and altruism. J. Evol. Biol. 19:1507–1516.
- Lehmann, L., F. Rousset, D. Roze, and L. Keller. 2007. Strong-reciprocity or strong-ferocity? A population genetic view of the evolution of altruistic punishment. Am. Nat. 170:21–36.
- Lehmann, L., M. W. Feldman, and F. Rousset. 2009. On the evolution of harming and recognition in finite panmictic and infinite structured populations. Evolution. doi: 10.1111/j.1558-5646.2009.00778.x *In press*.
- Mateo, J. M., and Johnston, R. E. 2000. Kin recognition and the ‘arm-pit effect’: evidence of self-referent phenotype matching. Proc. R. Soc. Lond. B 267:695–700.
- Maynard Smith, J. 1964. Group selection and kin selection. Nature 201:1145–1147.
- . 1976. Group selection. Q. Rev. Biol. 51:277–283.
- . 1982. Evolution and the theory of games. Cambridge Univ. Press, Cambridge.
- Maynard Smith, J., and E. Szathmari. 1995. The major transitions in evolution. W.H. Freeman, Oxford.
- Nowak, M. A. 2006. Five rules for the evolution of cooperation. Science 314:1560–1563.
- Okasha, S. 2002. Genetic relatedness and the evolution of altruism. Phil. Sci. 69:138–149.
- Owren, M. J., and J.-A. Bachorowski. 2001. The evolution of emotional expression: a “selfish-gene” account of smiling and laughter in early hominids and humans. Pp. 152–191 in T. J. Mayne and G. A. Bonanno, eds. Emotions: current issues and future directions. The Guilford Press, New York.
- Pepper, J. W., and B. Smuts. 2002. A mechanism for the evolution of altruism among nonkin: positive assortment through environmental feedback. Am. Nat. 160:205–213.
- Queller, D. C. 1984. Kin selection and frequency dependence: a game theoretic approach. Biol. J. Linn. Soc. 23:133–143.
- . 1985. Kinship, reciprocity and synergism in the evolution of social behaviour. Nature 318:366–367.
- Queller, D. C., E. Ponte, S. Bozzaro, and J. E. Strassmann. 2003. Single-gene greenbeard effects in the social amoeba *Dictostelium discoideum*. Science 299:105–106.
- Ridley, M., and A. Grafen. 1981. Are green beard genes outlaws? Anim. Behav. 29:954–955.
- Riley, M. A., and J. E. Wertz. 2002. Bacteriocins: evolution, ecology and application. A. Rev. Microbiol. 56:117–137.
- Riley, M. A., C. M. Goldstone, J. E. Wertz, and D. Gordon. 2003. A phylogenetic approach to assessing the targets of microbial warfare. J. Evol. Biol. 16:690–697.
- Ross, K. G., and L. Keller. 2002. Experimental conversion of colony social organization by manipulation of worker genotype composition in fire ants (*Solenopsis invicta*). Behav. Ecol. Sociobiol. 51:287–295.
- Rousset, F., and D. Roze. 2007. Constraints on the origin and maintenance of genetic kin recognition. Evolution 61:2320–2330.
- Seabright, P. 2004. The company of strangers: a natural history of economic life. Princeton Univ. Press, Princeton, NJ.
- Sinervo, B., and J. Clobert. 2003. Morphs, dispersal behavior, genetic similarity, and the evolution of cooperation. Science 300:1949–1951.
- Smukalla, S., M. Caldara, N. Pochet, A. Beauvais, S. Guadagnini, C. Yan, M. D. Vences, A. Jansen, M. Christine Prevost, J. Latge, et al. 2008. FLO1 is a variable greenbeard gene that drives biofilm-like cooperation in budding yeast. Cell 135:727–737.
- Summers, K., and B. J. Crespi. 2005. Cadherins in maternal-foetal interactions: red queen with a green beard? Proc. R. Soc. Lond. B 272:643–649.
- Taylor, P. D. 1992. Altruism in viscous populations—an inclusive fitness model. Evol. Ecol. 6:352–356.
- Turelli, M., and A. A. Hoffman. 1991. Rapid spread of an inherited incompatibility factor in California *Drosophila*. Nature 353:440–442.
- Werren, J. H. 1997. Biology of Wolbachia. Annu. Rev. Entomol. 42:587–609.
- West, S. A., A. S. Griffin, A. Gardner, and S. P. Diggle. 2006. Social evolution theory for microbes. Nat. Rev. Microbiol. 4:597–607.
- West, S. A., A. S. Griffin, and A. Gardner. 2007a. Evolutionary explanations for cooperation. Curr. Biol. 17:R661–R672.
- . 2007b. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. J. Evol. Biol. 20:415–432.
- White, C. E., and S. C. Winans. 2007. Cell-cell communication in the plant pathogen *Agrobacterium tumefaciens*. Phil. Trans. R. Soc. Lond. B 362:1135–1148.
- Wilson, D. S., and L. A. Dugatkin. 1997. Group selection and assortative interactions. Am. Nat. 149:336–351.
- Wilson, E. O., and B. Hölldobler. 2005. Eusociality: origin and consequences. Proc. Natl. Acad. Sci. USA 102:13367–13371.
- Wright, S. 1931. Evolution in Mendelian populations. Genetics 16:97–159.

Associate Editor: M. Rausher

## Appendix

### GREENBEARD DYNAMICS IN AN UNSTRUCTURED POPULATION

In the main text, we took an inclusive fitness approach to calculate conditions for when each type of greenbeard is expected to be favored by natural selection. Here, we recover these conditions using a more formal population genetics approach. We assume haploidy for simplicity, and divide the population into two types of individual: those carrying the greenbeard gene (G) and those who do not (N). The frequency of the two types are  $p$  and  $1 - p$ , respectively. We assume that all individuals pair at random to engage in social interactions, with a fecundity payoff  $P_{XY}$  accruing to an individual of type  $X \in (G, N)$  when interacting with an individual of type  $Y \in (G, N)$ . Each individual's fecundity  $F_{XY}$  is then given by a baseline unit, plus the payoff  $P_{XY}$  from their social interaction. Darwinian fitness is assumed to be proportional to the individual's fecundity.

The average fitness of greenbeard individuals is therefore given by

$$w_G = 1 + pP_{GG} + (1 - p)P_{GN}, \quad (\text{A1})$$

and the average fitness of nongreenbeard individuals is given by

$$w_N = 1 + pP_{NG} + (1 - p)P_{NN}. \quad (\text{A2})$$

The condition for the greenbeard to be selectively favored is  $w_G > w_N$ , or

$$p > \frac{P_{NN} - P_{GN}}{(P_{GG} - P_{NG}) + (P_{NN} - P_{GN})}, \quad (\text{A3})$$

where we assume that greenbeard individuals receive a greater payoff than nongreenbeards in encounters with greenbeard individuals ( $P_{GG} > P_{NG}$ ), and that nongreenbeard individuals receive a greater (or equal) payoff than greenbeards in encounters with nongreenbeard individuals ( $P_{NN} \geq P_{GN}$ ). This condition, given by Hamilton (1971), reveals the potential for greenbeards to experience frequency-dependent selection.

We now make explicit the helping and/or harming behavior and its fecundity impact on actor and recipient. We consider a generic greenbeard in which carriers help other greenbeard individuals, giving them a fecundity benefit  $b$  whilst incurring a personal fecundity cost  $c$ , and they harm nongreenbeard individuals, inflicting a fecundity cost  $d$  whilst incurring a personal fecundity cost  $a$ . We also denote the behavioral flexibility of individuals by  $f$ , and this takes values 0 or 1 for obligate or facultative greenbeards, respectively. Thus, the fecundity payoff for each type of interaction is given by:  $P_{GG} = b - c - (1 - f)a$ ,  $P_{GN} = -a - (1 - f)c$ ,  $P_{NG} = -d$  and  $P_{NN} = 0$ . Substituting these terms into condition (A3), we find that the generic greenbeard has a selective advantage if

$$p > \frac{a + (1 - f)c}{f(a - c) + b + d}, \quad (\text{A4})$$

where we assume  $b > c$  and  $d > a$ . This condition can be used to determine when each of the four basic types of greenbeard—facultative helping ( $a = d = 0, f = 1$ ), obligate helping ( $a = d = 0, f = 0$ ), facultative harming ( $b = c = 0, f = 1$ ), and obligate harming ( $b = c = 0, f = 0$ )—are selectively favored (conditions given in Table 2).

### Greenbeard Invasion in a Structured Population INTERACTIONS AMONG JUVENILES

Here, we derive invasion conditions for greenbeards in purely viscous populations, arriving at the results summarized in Table S1. We assume an infinite island population (Wright 1931) with  $n$  individuals per patch. We assume that each individual produces a large number  $K$  of offspring, and that social interaction

between juveniles within the patch determines the survival of juveniles to the dispersal phase of the lifecycle (below, we consider an alternative model in which social interaction between parents impacts upon fecundity, deriving the results presented in Table 3). Those juveniles surviving to the dispersal phase each have a probability  $m$  of independently dispersing to a random patch in the population, whereas the remainder  $1 - m$  stay on the natal patch. After dispersal,  $n$  juveniles are chosen at random to mature to adulthood and the rest are destroyed, i.e., density-dependent regulation operates after the dispersal event (hard selection) to return the patch to size  $n$ .

We assume the same payoffs as in the unstructured population model (above), but now we assume that each individual engages in a large number of pairings, spending an equal proportion of time interacting with each of the individuals on its patch, and that the payoff from each interaction is vanishingly small relative to the baseline, i.e.  $P_{XY} \ll 1$ . If  $I$  is the set of greenbeard individuals in the population, each assigned a unique index  $i \in I$ , then we can write the fecundity of the  $i$ th greenbeard individual as

$$F_i = 1 + p_i P_{GG} + (1 - p_i) P_{GN}, \quad (\text{A5})$$

where  $p_i$  is the local frequency of greenbeards on this individual's patch (including itself). Similarly, the average fecundity of all the individuals on the  $i$ th individual's patch is

$$\bar{F}_i = p_i F_i + (1 - p_i) F'_i, \quad (\text{A6})$$

where  $F'_i$  is the fecundity of each nongreenbeard individual in the patch, i.e.,:

$$F'_i = 1 + p_i P_{NG} + (1 - p_i) P_{NN}. \quad (\text{A7})$$

Owing to the rarity of the greenbeard gene, the average fecundity of all individuals in the population is  $\bar{F} = 1 + P_{NN}$ . The expected number of surviving offspring due to the focal greenbeard individual is therefore

$$w_i = m \frac{F_i}{\bar{F}} + (1 - m) \frac{F_i}{(1 - m) \bar{F}_i + m \bar{F}}. \quad (\text{A8})$$

Hence, averaging over all greenbeard individuals in the population, and neglecting higher-order terms of  $P_{XY}$ , the overall growth of the greenbeard gene in the population is given by

$$\begin{aligned} w_G = & 1 + E_I(p_i) P_{GG} + (1 - E_I(p_i)) P_{GN} \\ & - (1 - m)^2 (E_I(p_i^2) P_{GG} \\ & + (E_I(p_i) - E_I(p_i^2))(P_{GN} + P_{NG}) \\ & + (1 - 2E_I(p_i) + E_I(p_i^2)) P_{NN}) \\ & - (1 - (1 - m)^2) P_{NN}, \end{aligned} \quad (\text{A9})$$

where  $E_I$  denotes an expectation taken over the set of all greenbeard individuals. Note that, because greenbeards are present at



vanishingly low frequency in the population as a whole, then  $E_I(p_i) = r_P$  i.e., the coefficient of relatedness between randomly chosen offspring on a patch (Gardner and West 2006). Making this substitution, and defining  $E_I(p_i^2) = s_P$  (a clustering coefficient), we find that the greenbeard gene will invade the viscous population when  $w_G > 1$ , or

$$r_P P_{GG} + (1 - r_P) P_{GN} - (1 - m)^2 (s_P P_{GG} + (r_P - s_P)(P_{GN} + P_{NG}) + (1 - 2r_P + s_P) P_{NN}) - (1 - (1 - m)^2) P_{NN} > 0. \quad (A10)$$

Substituting in the fecundity effects defined in the unstructured population model (above), and rearranging, we obtain the invasion conditions given in Table A1 column 2. The relatedness and clustering coefficients can be expressed as functions of model parameters  $m$  and  $n$ , calculated below.

### INTERACTIONS AMONG ADULTS

Above, we considered that social interaction occurs among the numerous juveniles produced in each patch, and that the social effects impacted upon juvenile survival. We now assume that social interaction occurs among the  $n$  adults, and that the social effects impact upon their fecundity. This recovers the results summarized in Table 3. We follow the same procedure as before. First, we denote the set of all greenbeard individuals in the population as  $I$ , and assign each greenbeard individual a unique index  $i \in I$ . As before, the overall frequency of greenbeards on a focal greenbeard individual's patch is  $p_i = (1/n) + ((n - 1)/n)q_i$ , where  $q_i$  is the proportion of his patch mates that are also greenbeards. Rearranging we have  $q_i = (np_i - 1)/(n - 1)$ , and hence the fecundity of the focal greenbeard individual is

$$F_i = 1 + \frac{np_i - 1}{n - 1} P_{GG} + \left(1 - \frac{np_i - 1}{n - 1}\right) P_{GN}. \quad (A11)$$

Turning now to a nongreenbeard patch mate (if any exist) of the focal greenbeard individual, the proportion of his patch mates that carry the greenbeard gene is  $q'_i$  which satisfies  $p_i = ((n - 1)/n)q'_i$  and so  $q'_i = np_i/(n - 1)$ . This nongreenbeard individual therefore has fecundity

$$F'_i = 1 + \frac{np_i}{n - 1} P_{NG} + \left(1 - \frac{np_i}{n - 1}\right) P_{NN}, \quad (A12)$$

and the average fecundity on the focal greenbeard individual's patch is

$$\bar{F}_i = p_i F_i + (1 - p_i) F'_i. \quad (A13)$$

Again, owing to the rarity of the greenbeard gene, the average fecundity of all individuals in the population is  $\bar{F} = 1 + P_{NN}$ . The expected number of surviving offspring due to the focal greenbeard individual is therefore

$$w_i = m \frac{F_i}{\bar{F}} + (1 - m) \frac{F_i}{(1 - m) \bar{F}_i + m \bar{F}}. \quad (A14)$$

**Table A1. Invasion conditions for viscous populations (interactions among juveniles model). We assume the simplest model of population structure – Wright's (1931) infinite 'island' model, in which the population is subdivided into patches of  $n$  individuals, between which there is migration at rate  $m$  per individual per generation (and hence an average of  $M=mn$  migrants per patch per generation) – and that social behaviour among juveniles within patches mediates their survival to reproductive maturity. Column 2 lists exact invasion conditions for each type of greenbeard, calculated in the limit of weak selection. These depend on the within-patch relatedness coefficient,  $r_P=1/(n-(n-1)(1-m)^2)$ , and clustering coefficient,  $s_P=(n+2(n-1)(1-m)^2)/((n-(n-1)(1-m)^2)(n^2-(n-1)(n-2)(1-m)^3))$ . Column 3 expresses these invasion conditions in the limit of large patch size and low migration rate (i.e.,  $n \gg 1$ ,  $m \ll 1$ , and  $M$  on the order of 1).**

Greenbeard type	Invasion condition	
	Exact	Approximation
Helping, facultative	$\frac{b}{c} > 1$	$\frac{b}{c} > 1$
Helping, obligate	$\frac{b}{c} > \frac{1-(1-m)^2 r_P}{r_P - (1-m)^2 s_P}$	$\frac{b}{c} > 2+2M$
Harming, facultative	$\frac{d}{a} > \frac{1-r_P}{(1-m)^2 (r_P - s_P)} - 1$	$\frac{d}{a} > 1+2M$
Harming, obligate	$\frac{d}{a} > \frac{1-(1-m)^2 r_P}{(1-m)^2 (r_P - s_P)}$	$\frac{d}{a} > 2+2M$

Substituting equations (A11)–(A13) into equation (A14), applying a Taylor expansion, neglecting higher-order terms of  $P_{XY}$ , and averaging over the set  $I$  of all greenbeard individuals as before, we obtain

$$w_G = 1 + \frac{nr_P - 1}{n - 1} (P_{GG} - P_{GN}) + P_{GN} - (1 - m)^2 \left( \frac{ns_P - r_P}{n - 1} (P_{GG} - P_{GN}) + r_P P_{GN} + \frac{n}{n - 1} (r_P - s_P) (P_{NG} - P_{NN}) + (1 - r_P) P_{NN} \right) - (1 - (1 - m)^2) P_{NN}. \quad (A15)$$

Substituting in the fecundity effects defined in the unstructured population model (above), and rearranging, we recover the invasion conditions given in Table 3 column 2. The relatedness and clustering coefficients are defined in the usual way, and can be expressed as functions of model parameters  $m$  and  $n$ , calculated below.



RELATEDNESS AND CLUSTERING COEFFICIENTS

Above, we have derived invasion conditions for greenbeards in structured populations, and found that these are dependent upon the average greenbeard frequency (relatedness coefficient,  $r_P$ ), and average squared greenbeard frequency (clustering coefficient,  $s_P$ ), within patches—averaging over the set of all greenbeard individuals rather than over all patches in the population. We now calculate these coefficients in terms of the model parameters  $m$  and  $n$ .

First, we must describe aspects of the distribution of greenbeard individuals across patches in the population, and how this evolves over time. As above, we assign every greenbeard individual in the population a unique index  $i \in I$ . If we choose a greenbeard individual  $i$  at random, and denote the number of greenbeard individuals in its patch as  $j$ , then  $j$  is a random variable whose distribution depends on the genetic structure of the population. Note that  $j$  takes values from 1 to  $n$ , and that  $j/n = p_i$  is the local frequency of greenbeards in the  $i$ th individual's patch.

The distribution of  $j$  over the set  $I$  of greenbeards in any generation  $t$  can be denoted  $\psi_t(j)$  and (assuming that the greenbeard is vanishingly rare, and that it is selectively neutral relative to the nongreenbeard gene), its evolution is given by the recursion

$$\psi_{t+1}(j) = mX(j) + (1 - m) \sum_{k=1}^n \psi_t(k) \binom{n-1}{j-1} \times \left( (1 - m) \frac{k}{n} \right)^{j-1} \left( 1 - (1 - m) \frac{k}{n} \right)^{n-j}, \quad (A16)$$

where  $X(j) = 1$  for  $j = 1$  and 0 for all  $j \neq 1$ . With probability  $m$  the focal greenbeard individual is an immigrant, in which case it is guaranteed that they are the sole greenbeard on the patch (i.e.,  $j = 1$  with probability 1). With probability  $1 - m$  the focal greenbeard individual is native to the patch, in which case the probability of there being  $j$  greenbeards on the patch is the product of the probability of there having been  $k$  greenbeards on the patch in the previous generation (i.e.,  $\psi_t(k)$ ) and the probability that  $j - 1$  of the  $n - 1$  other individuals on the patch are also greenbeards (conditional upon  $k$ ), this being summed for all values of  $k$  from 1 to  $n$ . Any random juvenile produced in the patch by this parental generation has probability  $k/n$  of carrying the greenbeard gene, and it has probability  $1 - m$  of remaining in the patch rather than migrating. Thus, the number of other greenbeard individuals on the patch after dispersal and density-dependent regulation is binomially distributed with  $n - 1$  trials and probability of success  $(1 - m)k/n$ .

We define the equilibrium distribution as satisfying  $\psi(j) = \psi_{t+1}(j)$ , and this is given by

$$\psi(j) = mX(j) + (1 - m) \sum_{k=1}^n \psi(k) \binom{n-1}{j-1} \times \left( (1 - m) \frac{k}{n} \right)^{j-1} \left( 1 - (1 - m) \frac{k}{n} \right)^{n-j}, \quad (A17)$$

which has corresponding moment-generating function

$$M(z) = \sum_{j=1}^n e^{jz} \psi(j) = me^z + (1 - m) \sum_{k=1}^n \psi(k) e^z \left( 1 + (e^z - 1) (1 - m) \frac{k}{n} \right)^{n-1}. \quad (A18)$$

We obtain moments of  $j$  by differentiating  $M$  with respect to  $z$  the requisite number of times, and evaluating at  $z = 0$ . The first moment of  $j$  is given by  $E_t(j) = dM/dz|_{z=0}$ , or

$$E_t(j) = 1 + \frac{n-1}{n} (1 - m)^2 E_t(k). \quad (A19)$$

Noting that  $E_t(k) = E_t(j)$ , we can solve to obtain

$$E_t(j) = \frac{n}{n - (n-1)(1 - m)^2}. \quad (A20)$$

The relatedness coefficient is defined by  $r_P = E_t(j/n) = E_t(j)/n$ , which is given in the legend to Tables 3 and A1.

Similarly, the second moment is given by  $E_t(j^2) = d^2M/dz^2|_{z=0}$ , or

$$E_t(j^2) = 1 + 3 \frac{n-1}{n} (1 - m)^2 E_t(k) + \frac{n-1}{n} \frac{n-2}{n} (1 - m)^3 E_t(k^2). \quad (A21)$$

Because  $E_t(k) = E_t(j)$  and is given by equation (A20), and using the fact that  $E_t(k^2) = E_t(j^2)$ , we can solve equation (A21) to obtain

$$E_t(j^2) = \frac{n^2(n + 2(n-1)(1 - m)^2)}{(n - (n-1)(1 - m)^2)(n^2 - (n-1)(n-2)(1 - m)^3)}. \quad (A22)$$

The clustering coefficient is given by  $s_P = E_t((j/n)^2) = E_t(j^2)/n^2$ , and hence we arrive at the solution for  $s_P$  given in the legend to Tables 3 and A1.