

ARE GREENBEARDS INTRAGENOMIC OUTLAWS?

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Greenbeard genes identify copies of themselves in other individuals and cause their bearer to behave nepotistically toward those individuals. Hence, they can be favored by kin selection, irrespective of the degree of genealogical relationship between social partners. Although greenbeards were initially developed as a thought experiment, a number of recent discoveries of greenbeard alleles in real populations have led to a resurgence of interest in their evolutionary dynamics and consequences. One issue over which there has been disagreement is whether greenbeards lead to intragenomic conflict. Here, to clarify the “outlaw” status of greenbeards, we develop population genetic models that formally examine selection of greenbeard phenotypes under the control of different loci. We find that, in many cases, greenbeards are not outlaws because selection for or against the greenbeard phenotype is the same across all loci. In contrast, when social interactions are between genealogical kin, we find that greenbeards can be outlaws because different genes can be selected in different directions. Hence, the outlaw status of greenbeard genes crucially depends upon the particular biological details. We also clarify whether greenbeards are favored due to direct or indirect fitness effects and address the relationship of the greenbeard effect to sexual antagonism and reciprocity.

KEY WORDS: Chloropogonology, gestational drive, intragenomic conflict, kin selection, selfish gene, zygotic drive.

Natural selection favors those genes that are statistically associated with higher individual fitness (Fisher 1930; Price 1970). Genes can be associated with higher individual fitness in two ways: either by directly enhancing the reproductive success of their bearer (direct fitness) or by enhancing the reproductive success of other individuals who carry copies of the same genes (indirect fitness; Fisher 1930; Hamilton 1964). Hamilton (1964, 1970, 1975, 1996) argued that natural selection would lead organisms to appear designed to maximize their inclusive fitness, which is the sum of direct and indirect fitness (Grafen 2006a).

There are two basic mechanisms by which indirect fitness effects may arise (Hamilton 1964, 1975). First, individuals could aid genealogical kin who, owing to coancestry, are expected to share genes in common. This is the most common route by which

indirect benefits could accrue, and so the indirect consequences are often termed “kin selection” (Maynard Smith 1964). Second, individuals may provide benefits to those who share a particular gene in common, irrespective of their genealogical relationship. Dawkins (1976) illustrated this mechanism by imagining a gene that causes its bearer to grow a green beard and to behave altruistically toward other individuals with green beards; hence, such genes have become known as “greenbeards.” However, the fundamental requirement is an assortment mechanism that directs nepotistic behavior toward other carriers of the gene, rather than a phenotypic marker per se (Hamilton 1975). Furthermore, the greenbeard effect can operate by harming nonbearded individuals as well as by helping bearded individuals (Gardner and West 2004, 2010), and it can occur even when the beard and behavior

phenotypes are encoded by separate genes, provided these are in linkage disequilibrium (Haig 1997; Gardner and West 2010).

There has been disagreement over whether greenbeards are “outlaws” that conflict with other genes in the individual’s genome. Intragenomic conflict occurs when different loci in the same individual are selected in different directions (Burt and Trivers 2006). Many authors have suggested that greenbeards lead to intragenomic conflict because the genetic relatedness between actor and beneficiary can be much greater at the greenbeard locus than at other loci in the genome, and so altruistic helping could be favored at the greenbeard locus when it is disfavored at other loci (Alexander and Borgia 1978; Ridley and Grafen 1981; Dawkins 1982; Haig 1996; Okasha 2002; Helanterä and Bargum 2007; West et al. 2007b; Bourke 2011). However, Ridley and Grafen (1981) showed that a modifier gene, arising at another locus and fully suppressing the greenbeard phenotype, is only favored by selection in those contexts that disfavor the original greenbeard gene itself. This is because, although full suppression of the greenbeard phenotype saves “modified” individuals the cost of the social behavior, it also prevents them from benefiting from the behavior of fellow greenbeards.

The generality of this argument that greenbeards do not lead to intragenomic conflict remains unclear. Ridley and Grafen (1981) noted that a modifier gene that suppresses the behavior but retains the beard would always be favored, suggesting scope for intragenomic conflict (see Okasha 2002; Helanterä and Bargum 2007). However, Gardner and West (2010) argued that this does not lead to conflict, given that a “falsebeard” allele, arising at the greenbeard locus and having exactly the same effect as the partial suppressor, would also always be favored (hence selection acts identically at the greenbeard and modifier loci). These issues remain obscure while framed verbally, especially in light of additional complications raised by real-world examples of greenbeard genes. For example, different individuals may express the beard and the behavior (i.e., class structure; see Keller and Ross 1998), and there may be genealogical relationship (kinship) between social partners (Ridley and Grafen 1981; Haig 1996; Rice et al. 2008, 2009; Gardner and West 2010).

Here, we formally analyze if, when, and why greenbeards cause intragenomic conflict. Our first aim is to formally model Gardner and West’s (2010) verbal argument that a modifier arising elsewhere in the genome, fully or partially suppressing the greenbeard phenotype, will be favored or disfavored in accordance with a gene that arises at the greenbeard locus and gives rise to an identical phenotype. Specifically, we determine whether there is a mathematical analogy (isomorphism) between: (1) a two-locus model involving a greenbeard locus and a modifier locus, and (2) a one-locus model of greenbeard, nonbeard, and falsebeard alleles. Our second aim is to examine the impact of class structure and genealogical relationship between social partners. Our analyses

also allow us to formally classify greenbeard social behavior and to clarify conceptual links with other evolutionary phenomena, including sexual antagonism and reciprocity.

Models and Results

OVERVIEW OF ANALYSES

We use a formal population genetic approach, assuming populations of haploid individuals throughout. Each individual has a fixed phenotype that can be encoded by its allele at a greenbeard locus (one-locus model) or by a combination of alleles at the greenbeard locus and a modifier locus (two-locus model). The possible phenotypes are: greenbeard (G, i.e., expressing the beard and social behavior), nonbeard (N, i.e., expressing no beard and no behavior), and falsebeard (F, i.e., expressing the beard but eliminating the conditional behavior of greenbeards). Individuals interact in pairs, with a fecundity payoff P_{XY} accruing to individuals of type X when meeting a partner of type Y . This payoff, in addition to a baseline unit, determines the total fecundity of an individual with a given genotype. In this section, we outline the basic model of social interaction in a large, well-mixed population. Additional details for the models of class structure and interactions between kin are given in subsequent sections.

The goal of our analyses is to compare the direction of selection at the greenbeard locus (analysis of a one-locus model) with that at a modifier elsewhere in the genome (analysis of a two-locus model). If selection at these two places differs, then this indicates intragenomic conflict. For each of the three types of population structure analyzed (well-mixed, class structured, and kin-group structured), we consider two possible phenotype sets: one in which falsebeards cannot arise and the other in which falsebeards can arise. When considering the scenario in which falsebeards cannot arise, we assume that the greenbeard locus has only greenbeard (G) and nonbeard (N) alleles. The corresponding two-locus model has a greenbeard locus with G and N alleles and a modifier locus with modifier and nonmodifier alleles (μ and α , respectively), where, in this case, the modifier allele acts as a full suppressor (converting greenbeards to nonbeards). When considering the scenario in which falsebeards can arise, we assume that the greenbeard locus also has the falsebeard (F) allele and that the modifier allele acts as a partial suppressor (converting greenbeards to falsebeards). Table 1 provides an overview of these scenarios and the corresponding results.

We present our results below as conditions for a particular allele to be favored (derived in the Appendix). We will sometimes find it useful to write the condition in terms of Hamilton’s rule $rB > C$ (Hamilton 1964, 1970), where B is the effect of the behavior on the fitness of an individual’s social partner, C is the effect of the behavior on the actor’s own fitness, and r is the genetic relatedness between actor and recipient at the greenbeard

Table 1. Overview of model variants and results. For each of the population structures, we compare one- and two-locus models of two types: (1) when the phenotype set includes only greenbeards (G) and nonbeards (N), we compare selection for the N allele at a greenbeard locus with selection for a full-suppressing modifier at a second locus; (2) when the strategy set also includes a falsebeard (F), we compare selection for the F allele at a greenbeard locus with selection for a partial-suppressing modifier at a second locus. Conflicting selection pressures arise only when interactions are between genealogical relatives (kin) and only in contexts that favor unconditional helping ($Rb > c$, where R measures genealogical relationship, b is the fitness benefit to helped recipients, and c is the fitness cost to the helper).

Population structure	Phenotype set	Intragenomic conflict?
Well-mixed	{G,N}	No
	{G,N,F}	No
Class-structured	{G,N}	No
	{G,N,F}	No
Kin-group structured	$Rb < c$ {G,N}	No
	{G,N,F}	No
	$Rb > c$ {G,N}	No
	{G,N,F}	Yes

locus. The relatedness between greenbeards and nonbeards can be negative because average relatedness in a population is zero, by definition (Grafen 1985). Given that greenbeards can be positively related to one segment of the population (i.e., all greenbeard individuals), this must make them negatively related, on average, to the other segment (Gardner and West 2004, 2010). For example, in a population of greenbeard and nonbeard individuals (at frequencies p and $1 - p$, respectively), the relatedness of a greenbeard individual to the average member of the population (including himself) is $p \times 1 + (1 - p) \times r = 0$, where r is the relatedness to a nonbeard individual, given by $r = -p/(1 - p)$ (Gardner and West 2004, 2010).

In all scenarios, we consider four potential types of greenbeards (after Gardner and West 2010). First, the behavior of greenbeards can be helping or harming. Helping incurs a personal fecundity cost c to the actor and provides a fecundity benefit b to bearded recipients, whereas harming incurs a personal fecundity cost a to the actor and provides a fecundity cost d to nonbearded recipients (we assume $b > c$ and $d > a$). Second, a greenbeard's behavior can be obligate, whereby the behavior is enacted in all interactions (regardless of the beard status of partners), or else facultative, whereby the behavior is enacted only in interactions with greenbeards (in the case of helping) or nonbeards (in the case of harming). In addition to the costs associated with performing the behavior, we also consider that growing a beard incurs a fecundity cost k (this applies to both greenbeards and falsebeards).

Table 2. Payoffs (P_{XY}) to type X individuals (greenbeard [G], nonbeard [N], or falsebeard [F]) for interacting with type Y partners in a large, well-mixed population.

		Y		
		G	N	F
X	G	$b - c - k - (1 - f)a$	$a - k - (1 - f)c$	$c - k - (1 - f)a$
	N	$-d$	0	0
	F	$b - k$	$-k$	$-k$

Parameters: b = fecundity benefit to bearded recipients; c = personal fecundity cost of helping; d = fecundity cost inflicted on nonbearded recipients; a = personal fecundity cost of harming; k = fecundity cost of producing the beard; f = behavioral flexibility. For each type of greenbeard, payoffs are specified as follows: facultative helping: $a = d = 0$, $f = 1$; obligate helping: $a = d = 0$, $f = 0$; facultative harming: $b = c = 0$, $f = 1$; and obligate harming: $b = c = 0$, $f = 0$.

Table 2 gives the payoffs P_{XY} for all possible social interactions in a well-mixed population.

INTERACTIONS IN A WELL-MIXED POPULATION

Nonbeards and full-suppression.

We first consider the scenario of a well-mixed population and assume that falsebeards cannot arise. We ask: are the conditions that would favor a full-suppressing modifier equivalent to those that disfavor the greenbeard allele at its own locus? Starting with selection at the greenbeard locus (one-locus model), the absolute fitness of an allele encoding strategy $X \in \{G, N\}$ is

$$W_X = 1 + pP_{XG} + (1 - p)P_{XN}, \tag{1}$$

where p is the population frequency of greenbeard individuals. The conditions for greenbeards to be favored are derived in Table 3 and expressed in terms of a threshold value of b/c (for helping greenbeards) and d/a (for harming greenbeards). This leads us to derive:

Result 1: Costly beards ($k > 0$) are less readily favored than costless beards ($k = 0$). Higher cost k leads to an increasingly stringent condition for the greenbeard allele to be favored over the nonbeard allele, with the threshold values of b/c and d/a increasing in proportion to the value of k . Moreover, a costly greenbeard ($k > 0$) of any type is never able to invade a well-mixed population of nonbeards (Table 3; see Appendix for details).

We then consider selection at other loci by examining the corresponding two-locus model with a full-suppressing modifier. In this model, the absolute fitness of each genotype is

$$W_{G\mu} = 1 + p_{G\mu}P_{NN} + p_{G\alpha}P_{NG} + p_{N\mu}P_{NN} + p_{N\alpha}P_{NN} \tag{2}$$

$$W_{G\alpha} = 1 + p_{G\mu}P_{GN} + p_{G\alpha}P_{GG} + p_{N\mu}P_{GN} + p_{N\alpha}P_{GN} \tag{3}$$

Table 3. Conditions for selection to favor greenbeards in a large, well-mixed population of greenbeards (frequency p) and nonbeards (frequency $1 - p$). Parameters are as in Table 1. Note that changing the direction of the inequality gives the condition for nonbeards to be favored.

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

$$W_{N\mu} = 1 + p_{G\mu}P_{NN} + p_{G\alpha}P_{NG} + p_{N\mu}P_{NN} + p_{N\alpha}P_{NN} \quad (4)$$

$$W_{N\alpha} = 1 + p_{G\mu}P_{NN} + p_{G\alpha}P_{NG} + p_{N\mu}P_{NN} + p_{N\alpha}P_{NN}, \quad (5)$$

where p_X is the frequency of genotype X . We derive:

Result 2: A full-suppressing modifier is favored only when the greenbeard allele itself is disfavored. Conditions for the modifier to be favored (Table 4) are equivalent to the conditions for G to be disfavored in Table 3 (see Appendix for further details).

Result 2 formalizes the argument that selection for a full-suppressing modifier is equivalent to selection against the greenbeard at its own locus, implying no intragenomic conflict in this case (Ridley and Grafen 1981; Gardner and West 2010).

Falsebeards and partial suppression.

We now consider the same situation as above but allow falsebeards to arise. Our question is: are the conditions that would favor a partial-suppressing modifier equivalent to those that favor a falsebeard allele at the greenbeard locus? We start by examining selection at the greenbeard locus, using a one-locus model. The

Table 4. Conditions for selection to favor a full-suppressing modifier allele (which converts greenbeard individuals to nonbeards) in a large, well-mixed population. In these results from two-locus models, the frequency of individuals expressing the greenbeard phenotype (analogous to p in the one-locus model) is $\pi_G = p_G(1 - p_\mu)$. Results were approximated by a separation of timescales (see quasi-linkage equilibrium methods in the Appendix). Parameters are as in Table 1.

Greenbeard type	Condition to be favored
Helping, facultative	$\frac{b}{c} < 1 + \frac{k}{c\pi_G}$
Helping, obligate	$\frac{b}{c} < \frac{1}{\pi_G} + \frac{k}{c\pi_G}$
Harming, facultative	$\frac{d}{a} < \frac{1-\pi_G}{\pi_G} + \frac{k}{a\pi_G}$
Harming, obligate	$\frac{d}{a} < \frac{1}{\pi_G} + \frac{k}{a\pi_G}$

absolute fitness of an allele encoding strategy $X \in \{G, F, N\}$ is

$$W_X = 1 + pP_{XG} + qP_{XF} + (1 - p - q)P_{XN}, \quad (6)$$

where q is the population frequency of falsebeard individuals. The conditions for greenbeards to be favored are derived in Table 5. For helping greenbeards in particular, we define $\phi = p/(p + q)$ as the “reliability” of the beard, or the proportion of bearded recipients that share the greenbeard allele. It follows from the regression definition of relatedness (e.g., Grafen 1985) that the relatedness between a greenbeard actor and its bearded recipients is $r = (\phi - p)/(1 - p)$, where the average similarity between a greenbeard individual and the population is p , and the average similarity to himself is 1. It is also straightforward to show that, as above, the relatedness between greenbeards and their harmed (nonbearded) recipients is $r = -p/(1 - p)$.

Although greenbeards are favored if b/c or d/a exceed their threshold values, this advantage is short-lived when falsebeards can arise. The initial advantage of greenbeards eventually gives way to a disadvantage as falsebeards become common and diminish the beard’s reliability as an indicator of relatedness. The final outcome of selection depends upon whether the beard is costly. We derive:

Result 3: If beards are costless ($k = 0$), falsebeards are always favored when in the presence of greenbeards (i.e., when $p > 0$). In most cases, the final outcome of selection is a neutrally stable mixture of falsebeard and nonbeard alleles because the fecundity of falsebeards and nonbeards approach equality as greenbeards vanish ($W_F \rightarrow W_N$ as $p \rightarrow 0$; see Fig. S1). In the case of facultative harming, however, the fecundity of bearded individuals approaches equality as bearded individuals become common ($W_G \rightarrow W_F$ as $p + q \rightarrow 1$, i.e., as greenbeards cease to harm their social partners, making greenbeards and falsebeards effectively equivalent). Hence, in this case, a neutrally stable mixture of falsebeard and greenbeard alleles can be a final outcome (Fig. S1C; see Appendix for details).

Result 4: If beards are costly ($k > 0$), nonbeards are always favored as falsebeards become common, and in most cases, the nonbeard allele is ultimately fixed (Fig. S2). An exception occurs in the case of facultative harming, where the fecundity of falsebeard and greenbeard individuals approach equality as

Table 5. Conditions for selection to favor greenbeards in a large, well-mixed population of greenbeards (frequency p), falsebeards (frequency q), and nonbeards (frequency $1 - p - q$). The parameter $\phi = p/(p + q)$ represents the “reliability” of the beard (i.e., the proportion of bearded recipients that carry the greenbeard allele). All other parameters are as in Table 1.

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

$p + q \rightarrow 1$ (as above). If the greenbeard (G) allele is favored and remains favored as it and the falsebeard (F) allele spread, a neutrally stable mixture of F and G alleles can be a final outcome (Fig. S2C; see Appendix for details).

We then consider selection at other loci, by examining the corresponding two-locus model with a partial-suppressing modifier. In this model, the absolute fitness of each genotype is

$$W_{G\mu} = 1 + p_{G\mu}P_{FF} + p_{G\alpha}P_{FG} + p_{N\mu}P_{FN} + p_{N\alpha}P_{FN} \quad (7)$$

$$W_{G\alpha} = 1 + p_{G\mu}P_{GF} + p_{G\alpha}P_{GG} + p_{N\mu}P_{GN} + p_{N\alpha}P_{GN} \quad (8)$$

$$W_{N\mu} = 1 + p_{G\mu}P_{NF} + p_{G\alpha}P_{NG} + p_{N\mu}P_{NN} + p_{N\alpha}P_{NN} \quad (9)$$

$$W_{N\alpha} = 1 + p_{G\mu}P_{NF} + p_{G\alpha}P_{NG} + p_{N\mu}P_{NN} + p_{N\alpha}P_{NN} \quad (10)$$

We derive:

Result 5: If beards are costless ($k = 0$), the partial-suppressing modifier is usually favored. Starting with an all-greenbeard equilibrium ($p_G = 1, p_\mu = 0$) and assuming that the conditions for greenbeards to be favored are met, the modifier can invade a greenbeard population of any type except for facultative harming. This exception exists because, at equilibrium, no harming actually occurs and hence the modified phenotype is neutral. For all greenbeard types, equilibria with both greenbeard and modifier alleles at fixation ($p_G = p_\mu = 1$) are also neutrally stable, in this case because nonbeards (and facultative harming greenbeards) have the same fecundity as modified individuals (see Appendix for details).

Result 6: If beards are costly ($k > 0$), an increasing modifier frequency tends to favor the nonbeard allele at the greenbeard locus. Conditions for the modifier to invade a greenbeard population are equivalent to those in the costless beards ($k = 0$) scenario. But when beards are costly ($k > 0$), the modifier-fixed equilibria ($p_G = p_\mu = 1$) are never locally stable. As the modifier frequency increases, the nonbeard allele at the greenbeard locus is strongly favored and eventually reaches fixation (Fig.S3). However, an exception occurs when facultative harming greenbeards are favored; in this case, the greenbeard allele

can reach fixation with the modifier at a stable intermediate frequency (Fig. S3C; see Appendix for details).

Result 7: The dynamics of the one- and two-locus models are equivalent. When beards are costless ($k = 0$), both models usually predict a stable falsebeard population (or neutrally stable equivalent), and when beards are costly ($k > 0$), both models usually predict a stable nonbeard population. An exceptional case exists in both models, predicting the coexistence of falsebeards with facultative harming greenbeards (see Appendix for details).

Result 7 formalizes the argument that selection for a partial-suppressing modifier is equivalent to selection for a falsebeard allele at the greenbeard locus, implying no intragenomic conflict in this case (Gardner and West 2010).

INTERACTIONS IN A CLASS-STRUCTURED POPULATION

We now examine whether the conclusion that greenbeards do not lead to intragenomic conflict is changed by the complication of class structure. We assume that individuals of one class perform the behavior (and incur the associated cost) and individuals of the other class display the beard (and receive the benefit of help or the protection from harm). In this situation, a “full-suppressing” modifier could be selected to eliminate the costly behavior of greenbeard individuals in the behaving class, given that those individuals gain no benefit in return. More correctly, such a modifier should be recognized as a partial suppressor because it eliminates the behavior in one class but retains the beard in the other. Similarly, a type of falsebeard allele at the greenbeard locus could express the beard in one class (where fitness benefits accrue) but the nonbeard phenotype in the other, and selection for this allele may be equivalent to selection for the partial-suppressing modifier, implying no intragenomic conflict (Gardner and West 2010).

To formally address this, we extend a general version of our one-locus model of greenbeards in a well-mixed population to a simple case of class structure (see Grafen 2006b for a more general treatment of class structure). Individuals are assumed to grow up in randomly formed pairs, one as class A and the other as class B,

with only A individuals ever having the opportunity of performing a behavior, and only B individuals ever having the opportunity of receiving behavior. Hence, when two greenbeards interact, the A individual performs the costly social behavior whereas the B individual receives the help (or protection) associated with displaying the beard. Falsebeard individuals perform no social behavior when in the A class, but they produce a beard and may accrue benefits when in the B class. Fecundity payoffs for this population are given in Table S1.

Because individuals are in the A class with probability 1/2 and in the B class with probability 1/2, it follows that the absolute fitness of an allele encoding phenotype $X \in \{G, F, N\}$ is

$$W_X = (p/2)(P_{X_A G_B} + P_{X_B G_A}) + (q/2)(P_{X_A F_B} + P_{X_B F_A}) + [(1 - p - q)/2](P_{X_A N_B} + P_{X_B N_A}). \quad (11)$$

If the falsebeard phenotype does not exist ($q = 0$), the conditions for greenbeards to be favored in this model are the same as in the well-mixed population (Table 3); if falsebeards do exist ($q > 0$), the conditions are equivalent to those in Table 5. Conditions for falsebeards and nonbeards to be favored are similarly equivalent to earlier results from the well-mixed population. We derive:

Result 8: Class structure does not introduce intragenomic conflict. Results 2–7, which follow from a nonstructured population, also apply to the class-structured population. Selection for a full suppressor (eliminating the social behavior of A individuals and the beard of B individuals) or a partial suppressor (eliminating only the behavior of A individuals) is equivalent to selection for nonbeard or falsebeard alleles, respectively, in the one-locus model (eq. 11; see Appendix for details).

INTERACTIONS BETWEEN GENEALOGICAL RELATIVES

We now examine whether the conclusion that greenbeards do not lead to intragenomic conflict is changed by the complication of kin-group structure, where individuals interact in groups of genealogical relatives. We assume that a greenbeard gene causes its bearer to preferentially favor bearded kin at the expense of nonbearded kin. Such a greenbeard gene may be favored even if it reduces the total fecundity of its kin group, and for this reason, it has been regarded as an outlaw, analogous to a gene for meiotic drive (Ridley and Grafen 1981; see also Haig 1996; Rice et al. 2008, 2009). A favored greenbeard gene in kin groups has been implied to conflict with a full-suppressing modifier (eliminating the beard and the conditional behavior) in some cases (Ridley and Grafen 1981) and with a partial-suppressing modifier (eliminating the conditional behavior but retaining the beard) in others (Rice et al. 2008, 2009). Beyond these verbal arguments, however, there is a lack of formal models examining whether selection for a particular modifier type is equivalent to selection

at a greenbeard locus with the proper set of corresponding phenotypes.

To formally address this, we first analyze selection at the greenbeard locus (one-locus model) using methods for analyzing evolutionary games played between kin (e.g., Grafen 1979; Queller 1984). We assume that individuals pair at random within their social group to engage in social interactions. With probability R (the “others only” genealogical relatedness between two random individuals in a group), an individual interacts with a partner with the same phenotype (allele) because they are kin; with probability $1 - R$, the individual interacts with a partner whose phenotype depends on the population frequency of alleles. Payoffs from these interactions determine the fecundity of individuals, and crucially, we assume that all resulting offspring disperse completely from the group (i.e., global competition). More generally, the process that generates kinship within groups can also lead to local competition (reviewed by West et al. 2002). Gardner and West (2010) present a model of greenbeard evolution that incorporates kinship and local competition, but that model was not used to address the outlaw status of greenbeards.

To determine the “resident” nonbeard population to which greenbeards should be compared, we first consider when “defecting” (D; i.e., nonhelping) and unconditional helping (H) phenotypes are favored under the assumptions of our model. Let the H allele exist at population frequency p_H and the D allele exist at frequency $1 - p_H$. The absolute fitness of each allele is

$$W_H = 1 + RP_{HH} + (1 - R)[p_H P_{HH} + (1 - p_H)P_{HD}] = 1 + R.(b - c) + (1 - R)[p_H.(b - c) + (1 - p_H).(-c)] \quad (12)$$

$$W_D = 1 + RP_{DD} + (1 - R)[p_H P_{DH} + (1 - p_H)P_{DD}] = 1 + (1 - R)p_H b, \quad (13)$$

and we find that unconditional helping is favored when $Rb > c$. Hence, when $Rb < c$ the resident population should be made up of defectors, and when $Rb > c$ the resident population should be made up of unconditional helpers.

Throughout this section, we focus upon helping greenbeards (although their behavior may indirectly harm others—see below). This is because, given our demographic assumptions, (directly) harming greenbeards can never invade a population of defectors or unconditional helpers. Furthermore, it is straightforward to show that increasing genealogical relatedness only diminishes the conditions in which harming greenbeards can be favored.

Nonbeards and full suppression

We first consider selection at the greenbeard locus while only greenbeard and nonbeard alleles exist. Given a resident population of defectors (assuming $Rb < c$) or unconditional helpers

(assuming $Rb > c$), we introduce a helping greenbeard, at frequency p , as a conditional phenotype (e.g., help bearded kin only) and determine when it is favored. The absolute fitness of an allele encoding phenotype $X \in \{G, N\}$ is

$$W_X = 1 + RP_{XX} + (1 - R)[pP_{XG} + (1 - p)P_{XN}]. \quad (14)$$

Given the appropriate payoffs (Table S2), the greenbeard allele is favored over defecting nonbeards ($W_G > W_N$) when:

$$\frac{b}{c} > 1 + \frac{k}{c[p + (1 - p)R]} \quad (15)$$

for facultative helping greenbeards, and

$$\frac{b}{c} > \frac{1}{p + R} + \frac{k + pbR}{c(p + R)} \quad (16)$$

for obligate helping greenbeards. Hence, we derive:

Result 9: As genealogical relatedness increases, helping greenbeards are more readily favored over defecting nonbeards. In particular, increasing genealogical relatedness can allow helping greenbeards to invade a nonbeard population, unlike rare greenbeards in a well-mixed population (see Fig. S4A, for facultative helpers in particular). This occurs because, even though greenbeards are vanishingly rare in the global population, they can reach appreciable frequency (and therefore confer benefits on each other) within local kin groups.

The greenbeard allele is favored over unconditionally helping nonbeards when:

$$\frac{b}{c} > \frac{p - 1}{p} + \frac{k}{cp(1 - R)} \quad (17)$$

for facultative helping greenbeards, and

$$b > \frac{k}{p} + bR \quad (18)$$

for obligate helping greenbeards. Hence, we derive:

Result 10: If beards are costless ($k = 0$) and genealogical relatedness is less than unity ($R < 1$), helping greenbeards are always favored over unconditionally helping nonbeards. If beards are costly ($k > 0$), however, helping greenbeards are less readily favored (and less likely to invade from rarity) as genealogical relatedness (R) increases (see Fig. S4B, for facultative helpers in particular). The latter effect occurs because when genealogical relatedness is high, greenbeards have only a small probability of meeting (and withholding help from) nonbearded kin. Hence, greenbeards have minimal advantage over nonbeards, yet they still pay a cost for producing the beard.

We next examine selection at other loci, using a two-locus model of sexual haploids, to determine when a full-suppressing modifier can invade a population with a segregating greenbeard allele ($0 < p_G < 1$). “Full suppression” in this context means that when helping is not intrinsically favored ($Rb < c$), the modifier eliminates the beard and the helping behavior of greenbeards,

restoring defection among kin. When helping is intrinsically favored ($Rb > c$), the modifier eliminates the beard and the conditional behavior of greenbeards, restoring unconditional helping among kin. We assume that mating occurs randomly within the population, so interacting kin are related by one-half ($R = 1/2$). Comparing this model to the one-locus results, we derive:

Result 11: A full-suppressing modifier would invade only when the greenbeard allele is itself disfavored. A modifier that converts greenbeards to selfish nonbeards invades when $b/c < 1 + 2k/c(1 + p_G)$ and $b/c < [2(c + k)]/[c(1 + p_G)]$ for facultative and obligate helpers, respectively. Substituting p_G for p , these conditions are equivalent to the conditions for a greenbeard allele to be disfavored [see (15) and (16), respectively] at $R = 1/2$. A modifier that converts greenbeards to unconditional helpers can invade when $b/c < (p_G - 1)/p_G + 2k/cp_G$ and $b < 2k/p_G$ for facultative and obligate helpers, respectively. These conditions are equivalent to the conditions for a greenbeard allele to be disfavored [see (17) and (18), respectively] at $R = 1/2$ (see Appendix for details).

Hence, Result 11 shows that when interactions are among kin, selection for a full-suppressing modifier is equivalent to selection for a nonbeard allele at the greenbeard locus, implying no intragenomic conflict (contra Ridley and Grafen 1981).

Falsebeards and partial suppression.

Here, we consider interactions between kin while allowing falsebeards to exist. Considering selection at the greenbeard locus (one-locus model), we include a falsebeard allele, at frequency q , which encodes a phenotype of wearing the beard and otherwise behaving according to the appropriate resident population (i.e., according to the $Rb = c$ threshold). The absolute fitness of an allele encoding phenotype $X \in \{G, F, N\}$ is

$$W_X = 1 + RP_{XX} + (1 - R)[pP_{XG} + qP_{XF} + (1 - p - q)P_{XN}], \quad (19)$$

and the appropriate payoffs are given in Table S2.

When helping is not intrinsically favored ($Rb < c$), the following dynamics arise at the greenbeard locus. Facultative helping greenbeards invade a population of defectors when $b > k/R + c$, whereas an obligate helping greenbeard can never invade. These invasion conditions, in addition to the cost of the beard, determine the final outcome of selection. We derive:

Result 12: The falsebeard allele is always favored in the presence of greenbeards ($p > 0$), and if beards are costless ($k = 0$), the outcome may be a neutrally stable mixture of falsebeard and nonbeard alleles (Fig. S5A,C). If beards are costly ($k > 0$), the nonbeard allele is favored as falsebeards become common ($q \rightarrow 1$), with varying outcomes. When the greenbeard is an obligate helper, a stable population of defecting nonbeards evolves (Fig S5B). But when the greenbeard is a facultative helper and able to invade a population of defectors, selection leads to a stable cycling of phenotypes (Fig. S5D; see Appendix for details).

When helping is intrinsically favored ($Rb > c$), it is important to clarify the differences among phenotypes (see Table S2). First, an obligate helping greenbeard has the same fecundity as an unconditionally helping falsebeard, although nonbeards can accept the help of falsebeards only. Second, the key difference between a facultative helping greenbeard and a falsebeard is that whereas both receive help in all possible interactions, greenbeards save the cost of helping their nonbeard kin. The outcome of selection in these cases is:

Result 13: Obligate helping greenbeards (and falsebeards) are favored over nonbeards when $b > k/(1 - R)p$; otherwise, the nonbeard allele can be favored and approach fixation (Fig. S6A). On the other hand, facultative helping greenbeards are always favored, although the fitness of greenbeard and falsebeard alleles approach equality as bearded individuals become common (as $p + q \rightarrow 1$; Fig. S6B).

Finally, we consider selection at other loci by determining, with a two-locus model, the conditions in which a partial-suppressing modifier can invade a population with a segregating greenbeard allele ($0 < p_G < 1$). “Partial suppression” in this context means that when $Rb < c$, the modifier retains the beard but restores defection among kin; when $Rb > c$, the modifier retains the beard but restores unconditional helping. Comparing this model to the one-locus results, we derive:

Result 14: When helping is not intrinsically favored ($Rb < c$), a partial suppressor can always invade when $0 < p_G < 1$, consistent with falsebeard invasion in the one-locus model (Result 12; see Appendix for details).

Result 15: When helping is intrinsically favored ($Rb > c$), the conditions for a partial suppressor to invade can disagree with the one-locus model. When the greenbeard allele encodes an obligate helping greenbeard, a partial suppressor invades whenever $b > 0$. The dynamics of this model would then be equivalent to the one-locus case, with modified individuals (at frequency p_M) favored over nonbeards when $b > k/(1 - R)p_M$. When the greenbeard allele encodes a facultative helping greenbeard, the partial suppressor is always favored (the condition is $Rb > c$), and hence the modifier is always in conflict with a favored greenbeard allele at the greenbeard locus (see Appendix for details).

Result 15 therefore formalizes the description of greenbeard genes as “driving” agents when interactions are among kin (e.g., Ridley and Grafen 1981; Haig 1996; Rice et al. 2008, 2009). In this case, selection for a partial-suppressing modifier is not equivalent to selection for a falsebeard allele at the greenbeard locus, implying intragenomic conflict (contra Gardner and West 2010).

Discussion

Greenbeard genes are generally thought to be scarce in the real world, in part because their evolutionary interests can seem to con-

flict with the rest of the genome. We have shown that in many scenarios greenbeards are not in conflict with the rest of the genome: selection for and against greenbeard, nonbeard, and falsebeard phenotypes is often the same at greenbeard and modifier loci (Table 1). This holds in panmictic populations, in class-structured populations (where some individuals display the beard and others enact the behavior), and when considering full-suppressing modifiers (which eliminate both the beard and the behavior) in populations where genealogical relatives interact. The reason for this lack of conflict is that greenbeards are only favored at the greenbeard locus when the average benefit of carrying a greenbeard (e.g., being helped) outweighs the average cost of carrying a greenbeard (e.g., helping), in which case they also provide a benefit at the individual level (Ridley and Grafen 1981; Gardner and West 2010). Adding a production cost for the beard does not alter this conclusion, although it can lead to richer outcomes, including a cycling of phenotypes known as “rock-paper-scissors” dynamics (Maynard Smith 1982; Kerr et al. 2002).

In contrast, we found that when genealogical relatives interact and modifiers are able to eliminate conditional behavior (e.g., help all, not just fellow greenbeards) but retain the beard, then this can lead to conflict between loci over the greenbeard phenotype (Table 1). Conflict arises in contexts that favor unconditional helping, where Hamilton’s rule with genome-wide average relatedness ($Rb > c$) is satisfied. Here, a facultative helping greenbeard that withholds help from nonbearded neighbors can be favored. The corresponding falsebeard allele, which retains the beard but restores unconditional help to all neighbors, is not favored because (with certainty) nonbearded neighbors do not carry the falsebeard allele. However, a modifier arising elsewhere in the genome that retains the beard but restores unconditional help to all neighbors can be favored because, in this case, nonbearded neighbors may carry the modifier gene. This is only true if there is sex and recombination, so that genealogical kin who are identical at one locus (here, the modifier locus) need not be identical at other loci (here, the greenbeard locus). This scenario exemplifies true intragenomic conflict, where the same phenotype is selectively favored by one locus and selectively disfavored by another locus. Hence, greenbeards can sometimes be outlaws.

WHAT MAKES AN OUTLAW?

An outlaw gene has a positive selection coefficient at its own locus but, because of its negative effects on other loci, elicits suppression from modifier genes elsewhere in the genome (Dawkins 1982; Hurst et al. 1996; Burt and Trivers 2006). Given that a favored greenbeard allele always elicits partial suppression (creating a falsebeard phenotype), Bourke (2011) has suggested that all greenbeards can be considered outlaws. This interpretation, however, overextends the outlaw concept to cases that clearly do not involve intragenomic conflict. To illustrate this with a

simple example, consider a population where body size is well below its Darwinian optimum. A mutant gene that increases body size may be favored by selection, even if it slightly “overshoots” the optimum. As the new mutation spreads, selection may favor a “partial suppressing” modifier arising elsewhere in the genome, which reduces body size closer to the optimum. Yet, it would not be accurate to call the original mutant gene an outlaw because it is clear that the selection pressure to move the phenotype closer to the optimum is the same at both the body size and modifier loci.

Similarly, we emphasize that although a partial-suppressing modifier is always favored to convert greenbeards to falsebeards, a corresponding falsebeard allele at the greenbeard locus is also (usually) favored, implying no intragenomic conflict. The single case in which a falsebeard allele is not favored over its greenbeard allele stands out as a meaningful exception. This greenbeard allele, encoding a phenotype that withholds help from nonbeard kin, is a true outlaw that is strictly analogous to meiotic drivers and other selfish genetic elements (reviewed by Burt and Trivers 2006). An important caveat here is that, in making interlocus comparisons, we have assumed that the same phenotype set is available at greenbeard and modifier loci. That is, we have considered the selection pressure at each locus, not the actual genetic response to selection, which would depend upon the availability of genetic variation at that locus. This is consistent with the logic of genetic conflicts in general, where the idea is to consider how selection would act upon a hypothetical modifier arising in the genome, regardless of whether that modifier actually exists (Hurst et al. 1996).

What assumptions lead to the outlaw status of greenbeards that withhold help from genealogical relatives? Sexual reproduction plays the key role of generating variation among kin, with some carrying the greenbeard allele and others lacking it. Such variation is crucial because the advantage enjoyed by greenbeards depends entirely upon saving the cost of helping nonbeards; if there were no variation among kin, then there would be no scope for the greenbeard to be favored. Our models involving sex are relevant to the greenbeard effects implicated in “gestational drive,” where greenbeard mothers preferentially allocate resources to bearded embryos (Haig 1996) and “sexually-antagonistic zygotic drive,” where a gene for preferentially helping brothers, for example, could be favored if it arises on the Y chromosome (Rice et al. 2008, 2009). In particular, we clarify that the greenbeards in these cases would be outlaws from the perspective of a partially suppressing modifier. Real-life examples of greenbeard genes in sexual organisms, such as the Gp-9 gene of the red fire ant (Keller and Ross 1998), may represent true outlaw genes, whereas those examples from (primarily) asexual microbes (Queller et al. 2003; Smukalla et al. 2008) appear less likely to be outlaws.

GREENBEARDS, INCLUSIVE FITNESS MAXIMIZATION, AND SEXUAL ANTAGONISM

As a consequence of the greenbeard effect, individual organisms may not behave as strict maximizers of inclusive fitness. This is true of greenbeard individuals who withhold help from kin and also of greenbeard actors in well-mixed, class-structured populations who pay the cost of a social behavior only to benefit nonkin. However, because greenbeards rely on single (or tightly linked) genes, they are unlikely to give rise to striking adaptations (i.e., complex design; Gardner 2009). This contrasts with traits that provide a direct benefit, or an indirect benefit due to coancestry, both of which will lead to most of the genome striving in the same way to maximize inclusive fitness (Grafen 2006a). Consequently, we predict that the extent to which greenbeards prevent traits appearing designed to maximize inclusive fitness will be minor, even before we allow for the fact that greenbeard genes appear to be scarce (Gardner and West 2010; West and Gardner 2010).

Greenbeard genes in class-structured populations, where the gene can be beneficial for individuals in one class but detrimental for individuals in the other class, share similarities to genes in “intralocus sexual conflict” (reviewed by Bonduriansky and Chenoweth 2009), where an allele for a sexually homologous trait can be beneficial in one sex but detrimental in the other. In the absence of sex-limited expression, such sexually antagonistic alleles can be maintained in a population, resulting in individuals that appear unable to maximize their (inclusive) fitness. At the gene level, such behavior is understood by recognizing that the success of an allele must be averaged across the different classes that it finds itself in. But as with greenbeard genes in class-structured populations, genes in intralocus sexual conflict do not necessarily cause intragenomic conflict. Instead, both types of genes could be placed in an altogether different category of genes that erode the individual-as-maximizing agent analogy because of a constraint on the set of available phenotypes.

ARE GREENBEARDS ALTRUISTIC?

The helping behavior of greenbeards has typically been classified as altruistic, where greenbeard actors incur a personal cost for donating a benefit to fellow carriers (e.g., Lehmann and Keller 2006; West et al., 2007a,b; Gardner and West 2010; West and Gardner 2010). Similarly, greenbeard harming can be classified as spiteful, incurring a cost to the actor for inflicting a cost on nonbeard recipients (Gardner and West 2004, 2010). We followed this view by framing our results in terms of Hamilton’s rule, which partitions the inclusive fitness effects of a behavior into its direct fitness effects ($-C$) and indirect fitness effects (rB). The validity of this classification is evident in a class-structured population, where greenbeard individuals in the actor class are truly altruistic (or spiteful), incurring a lifetime personal fitness cost for their helping (or harming) behaviors.

However, it is also possible to classify greenbeards in terms of the fitness effects of the entire greenbeard complex, considering both the helping or harming behavior and the effects of displaying the beard (Foster 2009). This is possible when no class structure exists because, in that case, greenbeards also reap the benefit of help or the protection from harm; hence the greenbeard complex can be considered mutually beneficial (in the case of helping) or selfish (in the case of harming). Either classification is valid because of an ambiguity in how the causes of fitness effects are assigned to genes. When a greenbeard individual receives help, for example, one could decide that it was caused by the behavior component of the greenbeard gene in the social partner (implying an indirect fitness effect, consistent with altruism) or by the beard component of the recipient's own gene (implying a direct fitness effect, consistent with mutual benefit). By either perspective, only one of the gene's two effects—giving and attracting help—count toward an individual's inclusive fitness. From the first perspective, help received is ignored (assigned to the social partner) whereas help given is counted; from the second perspective, help given is ignored (treated as a side-effect of the beard) and help received is counted. In general, any fraction of the fitness effect of help can be assigned to direct versus indirect fitness.

IS THE GREENBEARD EFFECT DISTINCT FROM RECIPROCITY?

Helping behaviors that are encoded by greenbeard genes can seem similar to other examples of reciprocal cooperation. Both the greenbeard effect and reciprocity allow for mutually beneficial cooperation among nonkin, and both can be understood in terms of the direct fitness benefit to a helping individual. As with greenbeard genes, it is also possible to assign an indirect fitness benefit to a hypothetical gene for reciprocal cooperation (Nee 1989; Trivers 2006). In repeated interactions, for example, a gene for “tit for tat” (TFT; encoding initial cooperation followed by reciprocation of partners' actions; Axelrod and Hamilton 1981) would tend to direct help to other carriers of the TFT gene (other cooperators). Indeed, this TFT gene would be a type of greenbeard, where the helping behavior also acts as the beard.

However, there are two important caveats to recognize. First, it is highly unlikely that reciprocal helping in repeated interactions could be encoded by a single gene, or a number of genes in tight linkage disequilibrium, as required for TFT to be a greenbeard. So although TFT models may work owing to the greenbeard effect, real-world examples of TFT-like behavior probably would not involve greenbeard effects. Second, TFT could act as a greenbeard only in comparison to defectors that never cooperate—and it seems unlikely that TFT and defection would be the only possible phenotypes in any real population. It is relevant to note here that a TFT gene has been labeled as an outlaw, liable to suppression whenever unconditional helping is intrinsically favored ($Rb > c$;

Dugatkin et al. 1994). Yet given that unconditional helping should be the resident phenotype in this context, TFT could never be favored in the first place—it always helps, just as the resident does. In contrast, the “conventional” greenbeard is unique because it uses a separate but linked trait to direct help to fellow carriers. We have shown here that a such a greenbeard can invade a population of unconditional helpers, and we have clarified that, in certain conditions, it acts as a true outlaw.

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Appendix

ONE-LOCUS MODELS, WELL-MIXED POPULATION

The one-locus models follow the frequency of G, F, and N alleles, which we denote p , q , and $1 - p - q$, respectively. An allele encoding strategy X is favored when its absolute fitness (W_X , the average fecundity of its carriers) is greater than the average fitness of the population ($W_X > \bar{W}$, where $\bar{W} = pW_G + qW_F + (1 - p - q)W_N$). In the main text, these conditions are given in Table 3 (for $q = 0$) and Table 5 (for $q > 0$). Notice that a costly greenbeard ($k > 0$) of any type can never invade a nonbeard population: the threshold values of b/c (for helping greenbeards to be favored) and d/a (for harming greenbeards to be favored) go to infinity as $p \rightarrow 0$ (Tables 3, 5).

TWO-LOCUS MODELS, WELL-MIXED POPULATION

The two-locus models follow the change in genotype frequencies p_X , where $X \in \{G\alpha, N\alpha, G\mu, N\mu\}$ and $\sum p_X = 1$. We assume a life cycle of selection on haploid genotypes, random mating, recombination, and production of new haploid offspring. Following selection, the frequency of a given genotype is $p'_X = p_X W_X / \bar{W}$, where $\bar{W} = \sum p_X W_X$. Recursions for genotype frequencies in the next generation (p''_X) were derived in the usual way, by calculating the frequency of all possible mating pairs and adding the probabilities that each mating pair produces a given haploid genotype (not shown).

Here, we reframe these recursions into the multilocus notation of Barton and Turelli (1991), tracking greenbeard and modifier allele frequencies (p_G and p_μ , respectively) as well as the change in their statistical association (linkage disequilibrium, D). Following selection and recombination, the new variables are defined as

$$p''_G = p''_{G\mu} + p''_{G\alpha} \quad (A1)$$

$$p''_\mu = p''_{G\mu} + p''_{N\mu} \quad (A2)$$

$$D'' = p''_{G\mu} p''_{N\alpha} - p''_{G\alpha} p''_{N\mu}. \quad (A3)$$

Although still in terms of current genotype frequencies, we can express (A1, A2, A3) in terms of p_G , p_μ , and D by substituting the following:

$$p_{G\mu} = p_G p_\mu + D \quad (A4)$$

$$p_{G\alpha} = p_G(1 - p_\mu) - D \quad (A5)$$

$$p_{N\mu} = (1 - p_G)p_\mu - D \quad (A6)$$

$$p_{N\alpha} = (1 - p_G)(1 - p_\mu) + D. \quad (A7)$$

Given the appropriate p_G'' , we can now write model (A1, A2, A3) for a particular greenbeard and modifier type. For example, the dynamics of a facultative helping greenbeard and a full-suppressing modifier allele are:

$$p_G'' = \frac{p_G + \phi}{1 + \phi} \quad (A8)$$

$$p_\mu'' = \frac{p_\mu}{1 + \phi} \quad (A9)$$

$$D'' = (1 - z) \frac{(((\phi - 1)(D - (1 - p_G)p_\mu) - (D + p_G p_\mu)^2 + (D + p_G p_\mu)(1 + 2D - p_\mu - p_G(1 - 2p_\mu))))}{(1 + \phi)^2}, \quad (A10)$$

where $\phi = (k + (b - c)(D - p_G(1 - p_\mu)))(D - p_G(1 - p_\mu))$, and z is the recombination rate. Such a complicated system of nonlinear equations is difficult to analyze directly.

To simplify the analysis of this system, we use two techniques that lead to a quasi-linkage equilibrium (QLE) state (Kimura 1965), in which D settles to a nearly constant value (denoted by \hat{D}_Q). First, a QLE state is reached under the assumption that allele frequencies change by natural selection at a much slower rate than disequilibria change by recombination. Hence, this separation of timescales approach involves finding the quasi-equilibrium value of D (i.e., solving the condition $D'' = D = \hat{D}_Q$ for \hat{D}_Q) and then substituting \hat{D}_Q into the equations for allele frequency change.

The quasi-equilibrium cannot be found explicitly, however, and so we use a perturbation analysis that approximates \hat{D}_Q (see Otto and Day 2007, Ch. 9). Given the assumption that selection is weak, it follows that the parameters b , c , d , a , and k (fecundity increments) will be small values, denoted by multiplying each parameter by the small quantity δ . We then define $\hat{D}_Q = \hat{D}_0 + \hat{D}_1\delta + \hat{D}_2\delta^2 + \dots$ and write the quasi-equilibrium condition in the form $f(\delta) = 0$. Using equation (A10) as an example, we would write:

$$f(\delta) = (1 - z) \frac{(((\phi - 1)(\hat{D}_Q - (1 - p_G)p_\mu) - (\hat{D}_Q + p_G p_\mu)^2 + (\hat{D}_Q + p_G p_\mu)(1 + 2\hat{D}_Q - p_\mu - p_G(1 - 2p_\mu))))}{(1 + \phi)^2} - \hat{D}_Q, \quad (A11)$$

where $\phi = \delta(k + b - c)(\hat{D}_Q - p_G(1 - p_\mu))(\hat{D}_Q - p_G(1 - p_\mu))$ and \hat{D}_Q is defined as above. (Note that the form $f(\delta) = 0$ is achieved by subtracting \hat{D}_Q from the right-hand side of [A11]). By taking the Taylor series of $f(\delta)$ to first order in δ near the point $\delta = 0$,

$$f(\delta) = f(0) + \left(\frac{df}{d\delta} \Big|_{\delta=0} \right) \delta = 0, \quad (A12)$$

the terms in the approximation for \hat{D}_Q can be found by setting each term in (A12) to zero and solving for the \hat{D}_i . Returning to the

example in (A10), the first-order approximation of \hat{D}_Q in terms of the original parameters is

$$\hat{D}_Q \approx (1 - z) \frac{(1 - p_G)p_G(k - (b - c)p_G(1 - p_\mu))(p_\mu - 1)p_\mu}{-z}. \quad (A13)$$

Estimates for \hat{D}_Q were used to approximate modifier dynamics (Table 4 of the main text) and to plot the vector fields in Figure S3.

A QLE state is also attained in the context of a vanishingly rare gene invading an otherwise monomorphic

population (Gardner et al., 2007). Accordingly, we use local stability analyses as the second simplifying method for analyzing multilocus dynamics. As above, we substitute (A4, A5, A6) into (A1, A2, A3) to obtain a system of recursions for p_G , p_μ , and D . The Jacobian matrix for this model is defined as

$$\mathbf{J} = \begin{pmatrix} \frac{\partial p_G''}{\partial p_G''} & \frac{\partial p_G''}{\partial p_\mu''} & \frac{\partial p_G''}{\partial D''} \\ \frac{\partial p_\mu''}{\partial p_G''} & \frac{\partial p_\mu''}{\partial p_\mu''} & \frac{\partial p_\mu''}{\partial D''} \\ \frac{\partial D''}{\partial p_G''} & \frac{\partial D''}{\partial p_\mu''} & \frac{\partial D''}{\partial D''} \end{pmatrix}. \quad (A14)$$

When evaluated at an equilibrium, Equation (A14) provides a linear approximation of the dynamics near that equilibrium. If the absolute value of one of its eigenvalues λ_i is greater than unity, then the equilibrium in question is locally inviable.

When the modifier acts as a full suppressor of the greenbeard phenotype, we ask whether a monomorphic greenbeard

population is resistant to invasion by the modifier allele. We therefore evaluate (A14) with p_G at fixation and p_μ (and hence D) equal to zero. The leading eigenvalues in this case are:

$$\lambda = \frac{1}{1 + b - c - k} \quad (A15)$$

(for facultative and obligate helping green beards)

$$\lambda = \frac{1 - d}{1 - k} \quad (A16)$$

(for facultative harming green beards)

Table A1. Possible mating types and the genotypic distribution of offspring when a vanishingly rare modifier allele (μ ; nonmodifier is α) invades a population with a second, greenbeard locus having greenbeard (G) and nonbeard (N) alleles. For each mating type, we list the probability of a given allele finding itself in that mating type. Population frequencies are p_μ for the modifier allele ($1 - p_\mu$ for the nonmodifier) and p_G for the greenbeard allele ($1 - p_G$ for the nonbeard).

Mating type	Probability, from α allele's perspective	Probability, from μ allele's perspective	Genotypic distribution of offspring			
			αN	αG	μN	μG
1. $\alpha N \times \alpha N$	$(1 - p_G)^2(1 - p_\mu)$	0	1	0	0	0
2. $\alpha N \times \alpha G$	$2(1 - p_G)p_G(1 - p_\mu)$	0	1/2	1/2	0	0
3. $\alpha N \times \mu N$	$(1 - p_G)^2 p_\mu$	$(1 - p_G)^2(1 - p_\mu)$	1/2	0	1/2	0
4. $\alpha N \times \mu G$	$2(1 - p_G)p_G p_\mu$	$2(1 - p_G)p_G(1 - p_\mu)$	1/4	1/4	1/4	1/4
5. $\alpha G \times \alpha G$	$(p_G)^2(1 - p_\mu)$	0	0	1	0	0
6. $\alpha G \times \mu G$	$(p_G)^2 p_\mu$	$(p_G)^2(1 - p_\mu)$	0	1/2	0	1/2

$$\lambda = \frac{1 - d}{1 - k - a} \tag{A17}$$

(for obligate harming green beards).

Rearranging $\lambda > 1$ gives the conditions for the modifier to invade, consistent with the conditions given in Table 4 of the main text.

When the modifier acts as a partial suppressor of the greenbeard phenotype, we ask: (1) whether a monomorphic greenbeard population is resistant to invasion by the modifier allele, and (2) whether a population that is monomorphic for the greenbeard and modifier alleles is stable to invasion. Addressing point (1), the leading eigenvalues of (A14), evaluated at $p_G = 1$, $p_\mu = D = 0$, are:

$$\lambda = 1 + \frac{c}{1 + b - c - k} \tag{A18}$$

(for facultative and obligate helping greenbeards)

$$\lambda = 1 \text{ (for facultative harming greenbeards)} \tag{A19}$$

$$\lambda = \frac{1 - k}{1 - k - a} \tag{A20}$$

(for obligate harming greenbeards).

Hence, for all greenbeard types except facultative harming greenbeards, a partial suppressor can always invade as long as a and c take positive values; otherwise, the modifier is neutral (see Results 5 and 6 of the main text). To address point (2) above, we evaluate equation (A14) at $p_G = p_\mu = 1$ and $D = 0$. In this case, if beards are costless ($k = 0$), the leading eigenvalue is unity (for all greenbeard types), indicating a neutrally stable equilibrium (see Result 5). If beards are costly ($k > 0$), one eigenvalue is always equal to $1/(1 - k)$ (for all greenbeard types), indicating that the $p_G = p_\mu = 1$ equilibrium is never locally stable (Result 6 of the main text).

TWO-LOCUS MODEL, KIN-GROUP STRUCTURED POPULATION

Here, we consider a sexual haploid population that proceeds through the following life cycle: mating at random, production of a large number of haploid offspring, social interactions among randomly formed pairs of genealogical kin, and complete dispersal (and hence global competition). Given these assumptions, a focal individual shares an average “others-only” genealogical relatedness (R) of $1/2$ with its social partners. To simplify this model, we assume no linkage disequilibrium between greenbeard and modifier genes.

Selection acts on a greenbeard locus with alleles G (at frequency p_G) and N (frequency $1 - p_G$), and a modifier locus with alleles μ (modifier, frequency p_μ) and α (nonmodifier, frequency $1 - p_\mu$). We focus on the condition for a vanishingly rare modifier allele to invade a population that is fixed for the nonmodifier; hence, we need only consider μ/α and α/α mating types (see Table A1). As explained in the main text, the modifier allele may be a full suppressor or a partial suppressor, and its resulting phenotype (and the expected payoffs from social interaction) depends on the $Rb = c$ threshold. When $Rb < c$, modified individuals act as defectors, and carriers of the partial suppressor also display the beard. When $Rb > c$, modified individuals act as unconditional helpers, and carriers of the partial suppressor also display a beard. Here, we label the modifier phenotype M for generality; for any particular scenario, however, the appropriate phenotypes and payoffs are given in Table S2.

In this model, the absolute fitness (W) of an allele is calculated in the following manner. It is the probability of coming from a given parental mating type times the probability of the allele existing in an individual of a given genotype times the payoffs to that individual in all possible interactions within its kin group. From Table A1, these calculations involve mating types 3, 4, and 6 for the μ allele and mating types 1, 2, and 5 for the α allele:

$$\begin{aligned}
 W_{\mu} = & (1 - p_G)^2(1 - p_{\mu})P_{NN} + 2(1 - p_G)p_G(1 - p_{\mu})\left[\frac{1}{2}\left(\frac{1}{2}P_{NN}\right.\right. \\
 & \left. + \frac{1}{4}P_{NG} + \frac{1}{4}P_{NM}\right) + \frac{1}{2}\left(\frac{1}{2}P_{MN} + \frac{1}{4}P_{MG} + \frac{1}{4}P_{MM}\right)\left. \right] \\
 & + p_G^2(1 - p_{\mu})\left(\frac{1}{2}P_{MM} + \frac{1}{2}P_{MG}\right) \tag{A21}
 \end{aligned}$$

$$\begin{aligned}
 W_{\alpha} = & (1 - p_G)^2(1 - p_{\mu})P_{NN} + 2(1 - p_G)p_G(1 - p_{\mu})\left[\frac{1}{2}\left(\frac{1}{2}P_{NG}\right.\right. \\
 & \left. + \frac{1}{2}P_{NN}\right) + \frac{1}{2}\left(\frac{1}{2}P_{GG} + \frac{1}{2}P_{GN}\right)\left. \right] + p_G^2(1 - p_{\mu})P_{GG} \tag{A22}
 \end{aligned}$$

In equation (A21), for example, the μ allele comes from mating type 3 with probability $(1 - p_G)^2(1 - p_{\mu})$, finds itself in a nonbeard individual with probability one, and always interacts

with another nonbeard (first term). It comes from mating type 4 with probability $2(1 - p_G)p_G(1 - p_{\mu})$, finds itself in a nonbeard individual half of the time and in a “modified” individual the other half, and in both cases, those individuals interact with nonbeards, greenbeards, and other modified individuals with frequency 1/2, 1/4, and 1/4, respectively (second term). Finally, the μ allele comes from mating type 6 with probability $p_G^2(1 - p_{\mu})$ and always finds itself in a modified individual who interacts with modifier and greenbeard strategies with equal frequency (third term). The absolute fitness of the α allele follows in similar fashion.

Given the appropriate modifier phenotype and associated payoffs (Table S2), we find the conditions $W_{\mu} > W_{\alpha}$, as reported in Results 11 and 13 of the main text.

Supporting Information

The following supporting information is available for this article:

Figure S1. The direction of selection acting at a locus encoding greenbeard (G), falsebeard (F), and nonbeard (N) phenotypes, where the production of beards is costless ($k = 0$).

Figure S2. The direction of selection acting at a locus encoding greenbeard (G), falsebeard (F), and nonbeard (N) phenotypes, where the production of beards is costly ($k = 0.1$ in all panels).

Figure S3. The direction of selection, approximated at quasi-linkage equilibrium, acting at two loci: a greenbeard locus, with greenbeard allele at frequency p_G , and a modifier locus, with partial-suppressor allele at frequency p .

Figure S4. Frequency-dependent selection on facultative helping greenbeards in a population of kin groups with average genealogical relationship R .

Figure S5. The direction of selection acting at a locus encoding greenbeard (G), defecting falsebeard (F), and defecting nonbeard (D) phenotypes in a structured population of kin groups, where it is assumed that $Rb < c$ ($b = 0.6$, $c = 0.35$, $R = 0.5$).

Figure S6. The direction of selection acting at a locus encoding facultative or obligate helping greenbeard (G), unconditionally helping falsebeard (F), and unconditional helping nonbeard (H) phenotypes in a structured population of kin groups, where it is assumed that $Rb > c$ ($b = 0.6$, $c = 0.25$, $R = 0.5$).

Table S1. Payoffs (P_{XY}) to type X individuals (greenbeard [G], nonbeard [N], or falsebeard [F]) for interacting with type Y partners in a class-structured population of individuals that can only ever perform a behaviour (class A) or only ever receive the behaviour (class B).

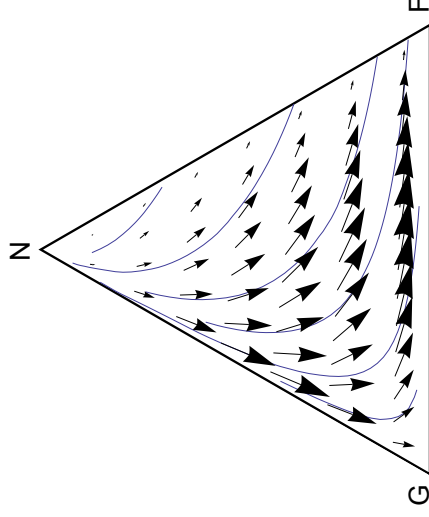
Table S2. Payoffs (P_{XY}) to type X individuals (helping greenbeard [G], nonbeard [N], or falsebeard [F]) for interacting with type Y partners in kin groups.

Supporting Information may be found in the online version of this article.

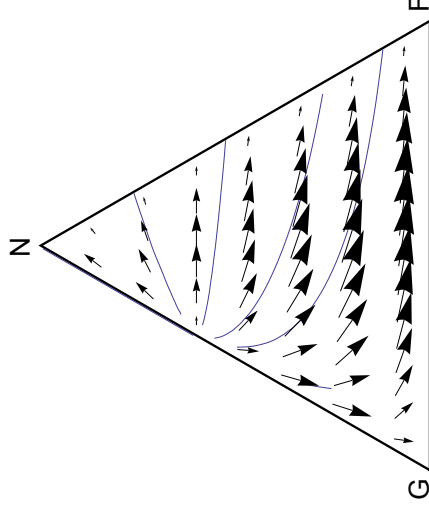
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Supporting Information (Figures 1-6; Tables 1 & 2)

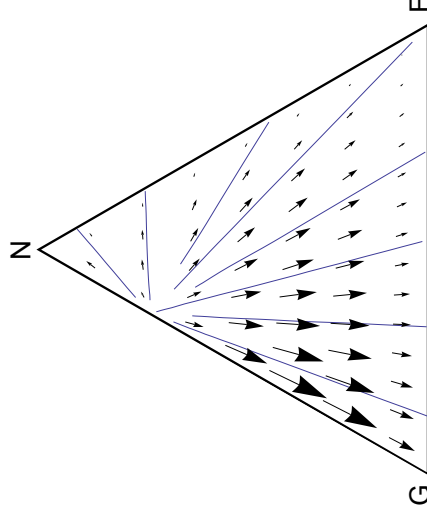
A. Facultative helping



B. Obligate helping



C. Facultative harming



D. Obligate harming

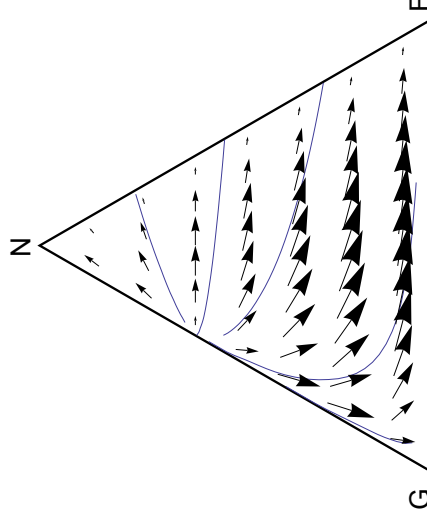


Figure 1. The direction of selection acting at a locus encoding greenbeard (G), falsebeard (F), and nonbeard (N) phenotypes, where the production of beards is costless ($k = 0$). The corners of each triangle represent populations in which the corresponding phenotype (allele) is fixed, and the size of arrows represents the strength of selection. In panels A, B, and D, the outcome may be a neutrally stable mixture of falsebeards and nonbeards, whereas in panel C, the outcome may be a neutrally stable mixture of falsebeards and greenbeards or falsebeards and nonbeards. Other parameters used: in A: $b = 0.5$, $c = 0.2$, $f = 1$; in B: $b = 0.5$, $c = 0.2$, $f = 0$; in C: $d = 0.5$, $a = 0.2$, $f = 1$; in D: $d = 0.5$, $a = 0.2$, $f = 0$.

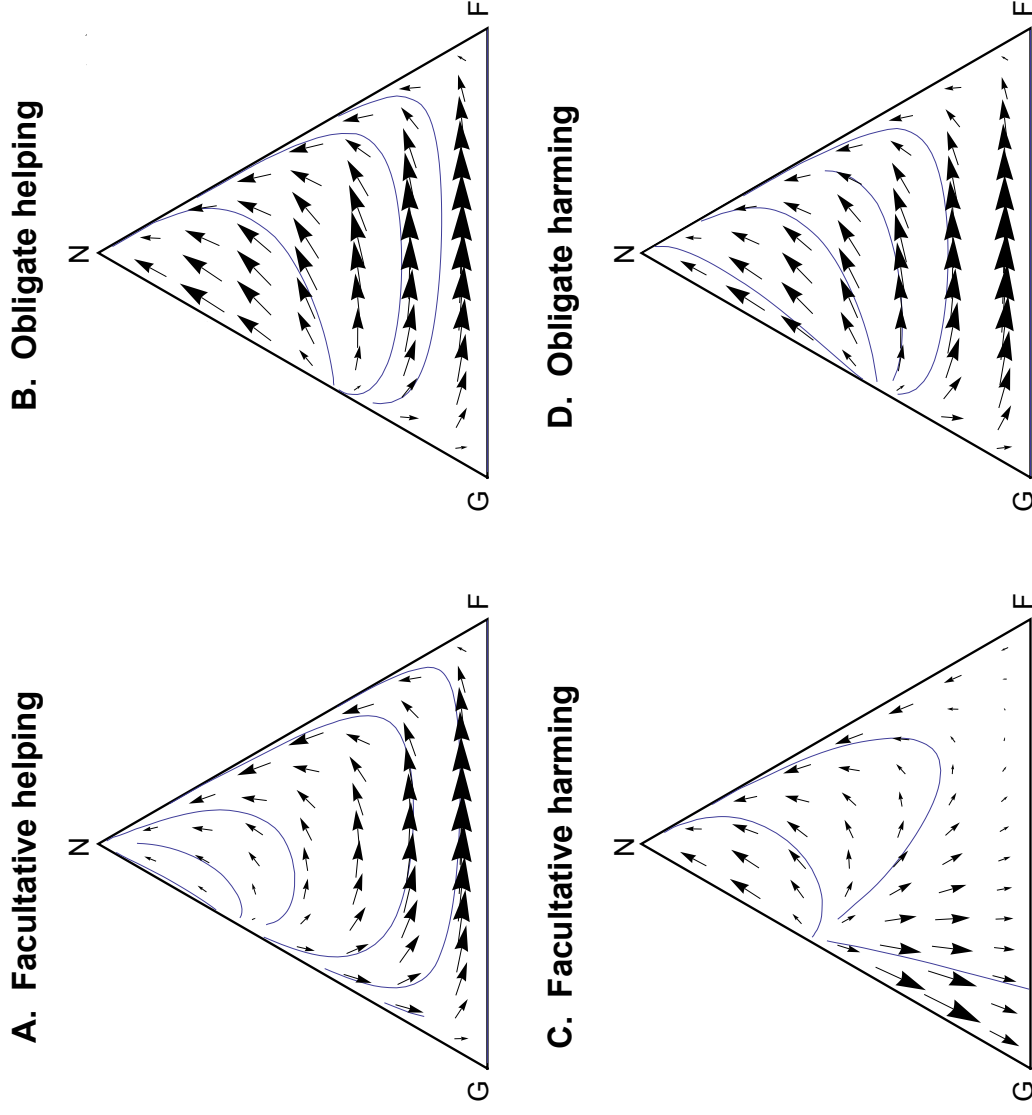


Figure 2. The direction of selection acting at a locus encoding greenbeard (G), falsebeard (F), and nonbeard (N) phenotypes, where the production of beards is costly ($k = 0.1$ in all panels). The corners of each triangle represent populations in which the corresponding phenotype (allele) is fixed, and the size of arrows represents the strength of selection. In panels A, B, and D, the outcome of selection is a population of nonbeards, whereas in panel C, the outcome may also be a neutrally stable mixture of falsebeards and greenbeards, depending on initial conditions. All other parameters are as in Figure 1.

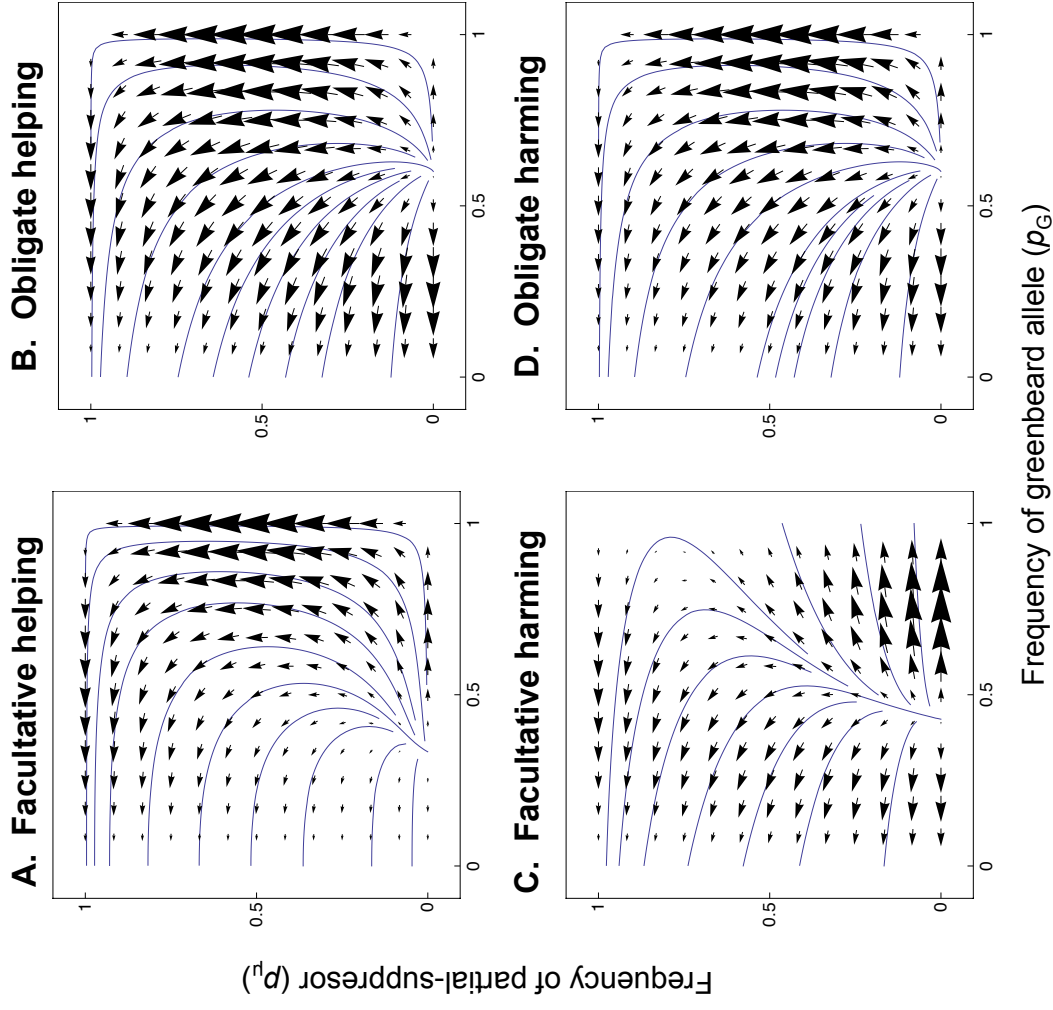


Figure 3. The direction of selection, approximated at quasi-linkage equilibrium, acting at two loci: a greenbeard locus, with greenbeard allele at frequency p_G , and a modifier locus, with partial-suppressor allele at frequency p_μ . In panels A, B, and D, the outcome of selection is a population fixed for the nonbeard allele, whereas in C, the outcome can be a mixture of greenbeards and “modified” greenbeards (expressing a falsebeard phenotype). Parameters used: $k = 0.1$; recombination rate, $z = 0.5$; all others are as in Figure 1.

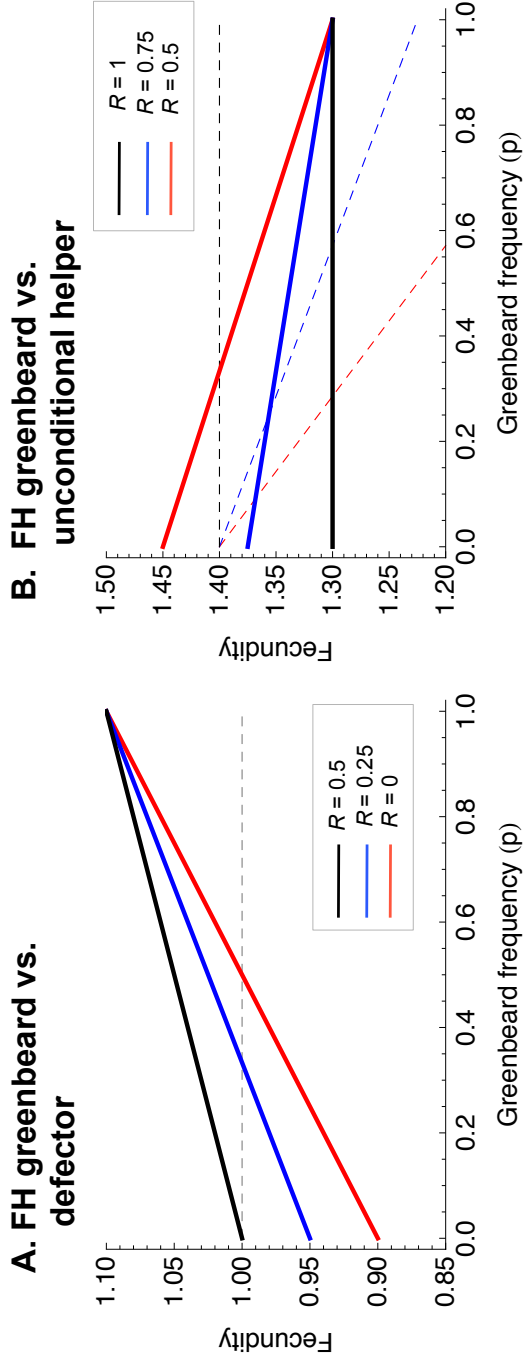


Figure 4. Frequency-dependent selection on facultative helping greenbeards in a population of kin groups with average genealogical relatedness R . Solid lines represent the fecundity of greenbeards, and the corresponding dotted lines represent the fecundity of competing nonbeards. In panel A, it is assumed that $Rb < c$ ($b = 0.5$, $c = 0.3$, $k = 0.1$), and increasing R is shown to favour greenbeards over defecting nonbeards. In panel B, it is assumed that that $Rb > c$ ($b = 0.7$, $c = 0.3$, $k = 0.1$), and increasing R is shown to disfavour greenbeards over unconditionally helping nonbeards. Note that the mean fecundity of a monomorphic nonbeard population would be 1.0 in A and 1.4 in B.

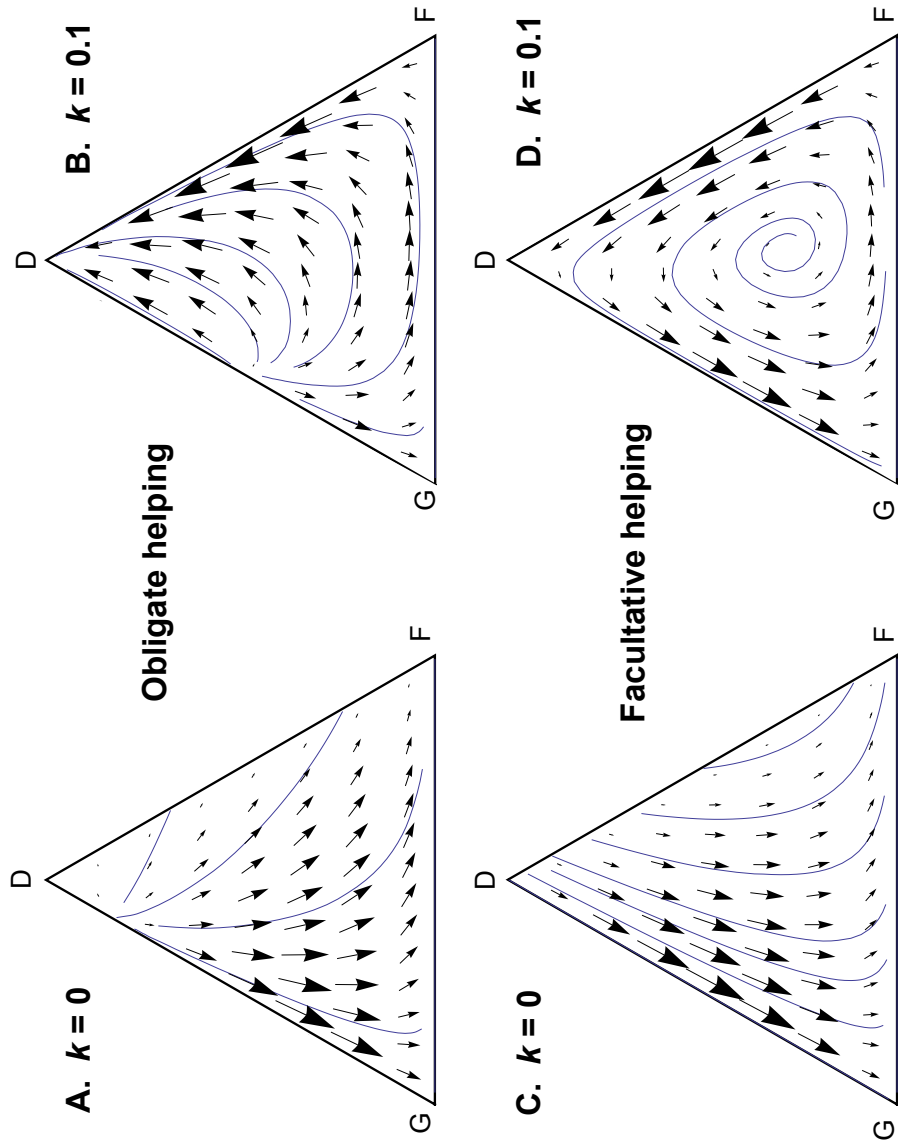
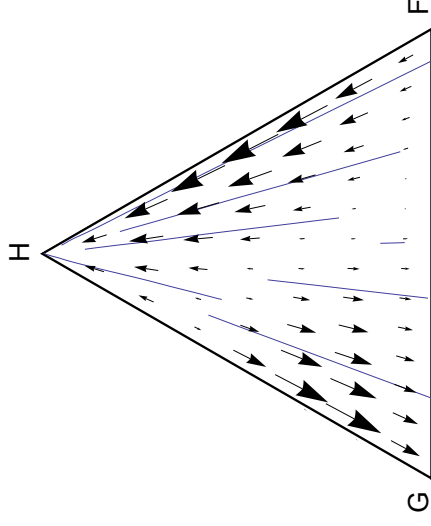


Figure 5. The direction of selection acting at a locus encoding greenbeard (G), defecting falsebeard (F), and defecting nonbeard (D) phenotypes in a structured population of kin groups, where it is assumed that $Rb < c$ ($b = 0.6, c = 0.35, R = 0.5$). If beards are costless ($k = 0$), the outcome of selection is a neutrally stable mixture of falsebeards and defecting nonbeards (panels A, C). If beards are costly ($k > 0$), however, selection can lead to a stable population of defectors (panel B) or to a stable cycling of all three phenotypes (panel D).

A. Obligate helping



B. Facultative helping

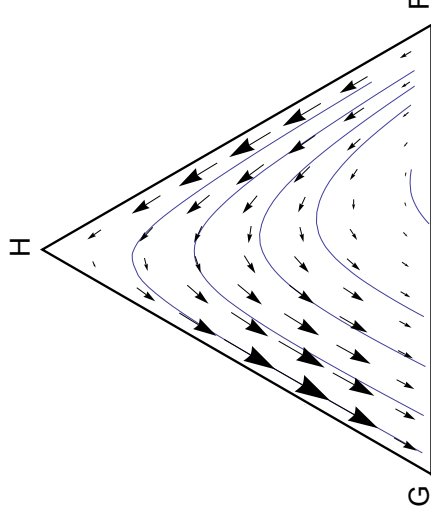


Figure 6. The direction of selection acting at a locus encoding facultative or obligate helping greenbeard (G), unconditionally helping falsebeard (F), and unconditional helping nonbeard (H) phenotypes in a structured population of kin groups, where it is assumed that $Rb > c$ ($b = 0.6$, $c = 0.25$, $R = 0.5$). Because the beard is costly ($k = 0.1$), helping nonbeards can be favoured over falsebeards in all cases. In panel A, unconditional helping can ultimately become fixed, but otherwise, selection favours greenbeards, leading to a neutrally stable mixture of greenbeards and falsebeards (panels A, B).

Table 1. Payoffs (P_{XY}) to type X individuals (greenbeard [G], nonbeard [N], or falsebeard [F]) for interacting with type Y partners in a class-structured population of individuals that can only ever perform a behaviour (class A) or only ever receive the behaviour (class B). Note that only greenbeard and falsebeard individuals in class B pay the cost of producing a beard (k). All other parameters are as in Table 1 of the main text.

		Y					
		G_A	N_A	F_A	G_B	N_B	F_B
X	G_A	-	-	-	$-c - (1-f)a$	$-a - (1-f)c$	$-c - (1-f)a$
	N_A	-	-	-	0	0	0
	F_A	-	-	-	0	0	0
	G_B	$b - k$	$-k$	$-k$	-	-	-
	N_B	$-d$	0	0	-	-	-
	F_B	$b - k$	$-k$	$-k$	-	-	-

Table 2. Payoffs (P_{XY}) to type X individuals (helping greenbeard [G], nonbeard [N], or falsebeard [F]) for interacting with type Y partners in kin groups. When helping is not intrinsically favoured ($Rb < c$), the nonbeard is a defector (D). When helping is intrinsically favoured ($Rb > c$), the nonbeard is an unconditional helper (H). Parameters are as in Table 1 of the main text.

		$Rb < c$			$Rb > c$		
		G	N (D)	F	G	N (H)	F
X	G	$b - c - k$	$-(1 - f)c - k$	$-c - k$	$b - c - k$	$b - (1 - f)c - k$	$b - c - k$
	F	$b - k$	$-k$	$-k$	$b - c - k$	$b - c - k$	$b - c - k$
	N	0	0	0	$-c$	$b - c$	$b - c$