LETTER

The relation between R. A. Fisher's sexy-son hypothesis and W. D. Hamilton's greenbeard effect

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Recent years have seen a growing interest in the overlap between the theories of kin selection and sexual selection. One potential overlap is with regards to whether R. A. Fisher's "sexy-son" hypothesis, concerning the evolution of extravagant sexual ornamentation, may be framed in terms of W. D. Hamilton's greenbeard effect, concerning scenarios in which individuals carry an allele that allows them to recognize and behave differently toward other carriers of the same allele. Specifically, both scenarios involve individuals behaving differently toward social partners who exhibit a phenotypic marker, with linkage disequilibrium between marker and behavior loci ensuring genetic relatedness between actor and recipient at the behavior locus. However, the formal connections between the two theories remain unclear. Here, we develop these connections by: (1) asking what kind of greenbeard is involved in the sexy-son hypothesis; (2) exploring the relationship between the problem of "falsebeards" and the "lek paradox"; (3) investigating whether these two problems may be resolved in analogous ways; and (4) determining whether population structure facilitates both of these evolutionary phenomena. By building this conceptual bridge, we are able to import results from the field of kin selection to sexual selection, and vice versa, yielding new insights into both topics.

KEY WORDS: falsebeard, Fisher's runaway, kin selection, lek paradox, linkage disequilibrium, mating preference, population genetics, population structure, sexual selection.

Impact Summary

In this article, we investigate the connections between two classic ideas about evolutionary biology. First, the "greenbeard effect"–described by W. D. Hamilton in 1964, and later given its name by Richard Dawkins in *The Selfish Gene*–is the idea that if a gene can cause the display of a conspicuous marker, such as making its carriers grow green beards, and also cause its carriers to act altruistically toward fellow bearers of green beards, then it can be favored by natural selection because it is ultimately helping copies of itself. Second, the "sexy son" effect–described by R. A. Fisher in 1915–is the

idea that females will be favored to preferentially mate with males who exhibit conspicuous ornamentation if other females already happen to find this ornamentation attractive, simply because by mating with ornamented males they are more likely to have ornamented sons who will be more attractive to potential mating partners. Here, we show: (1) that the sexy-son effect is a special case of the greenbeard effect; (2) what kind of greenbeards are involved in the sexy-son effect; (3) that ideas about how new mutations fuel the sexy-son effect also provide a solution to the long-standing problem of "falsebeards," which is when some individuals cheat by

growing a green beard but without enacting any altruism; and (4) that low rates of dispersal, which are already known to promote the greenbeard effect, also allow the sexy-son effect to get started in the first place.

Both kin selection and sexual selection have been subjected to decades of intense research. Unfortunately, these fields have developed largely independently of each other, with there being relatively little exchange of ideas and insights between the two literatures (Cronin 1993; Boomsma 2007; Pizzari and Gardner 2012). But recently the overlap between these topics has begun to be explored in some detail, both theoretically and empirically, and with a particular focus on how kin selection may modulate sexual conflicts (Rankin 2011; Wild et al. 2011; Pizzari and Gardner 2012; Carazo et al. 2014; Chippindale et al. 2015; Pizzari et al. 2015; Faria et al. 2015, 2017; Hollis et al. 2015; Martin and Long 2015; Tan et al. 2017; Le Page et al. 2017; Łukasiewicz et al. 2017; Lymbery and Simmons 2017).

W. D. Hamilton (1963, 1964) pointed out that there are three basic mechanisms for generating kin selection, and each of these has received some attention with regard to sexual selection. First, "population viscosity"–whereby some individuals do not disperse and hence tend to be genetically related to their neighbors, such that even indiscriminate social behavior may give rise to kin-selection effects (1963, 1964)–has been explored in relation to sexual conflict, both theoretically (Rankin 2011; Wild et al. 2011; Pizzari and Gardner 2012; Faria et al. 2015, 2017; Pizzari et al. 2015) and empirically (Łukasiewicz et al. 2017). Second, "kin recognition"–whereby individuals may identify their genealogical relatives and adjust their social behavior accordingly (1963, 1964)–has also been explored in relation to sexual conflicts, both theoretically (Pizzari and Gardner 2012) and empirically (Carazo et al. 2014; Chippindale et al. 2015; Hollis et al. 2015; Martin and Long 2015; Le Page et al. 2017; Tan et al. 2017).

Third, "greenbeard effects"–whereby individuals carry an allele that allows them to recognize and behave differently toward other carriers of the same allele (Hamilton 1964; Dawkins 1976; Gardner and West 2010)–have been discussed in relation to sexual selection by Dawkins (1986) and Pizzari and Gardner (2012), with regards to whether R. A. Fisher's "sexy-son" hypothesis–concerning the evolution of extravagant sexual ornamentation (Fisher 1915, 1930; Weatherhead and Robertson 1979)–may be framed in terms of a greenbeard effect. Specifically, both scenarios appear to involve individuals behaving differently toward social partners who exhibit a phenotypic marker, with linkage disequilibrium between marker and behavior loci ensuring genetic relatedness between actor and recipient with respect to the be-

havior locus (Box 1). However, the formal connections between these two theories remain unclear.

Here, we investigate the theoretical connections between Fisher's (1915, 1930) sexy-son effect and Hamilton's (1964) greenbeard effect to determine the extent to which these two ideas coincide, and to see whether prior insights that have emerged in relation to each effect may have useful analogs in relation to the other. First, we draw upon Gardner and West's (2010) classification of helping versus harming and facultative versus obligate greenbeards to ask: if the sexy-son hypothesis is to be framed in terms of the greenbeard effect, then what kind of greenbeard is involved? Second, we determine whether the evolutionary dynamics of the sexy-son effect mirror those of the greenbeard effect, and explore the relationship between the "lek paradox" (Borgia 1979) and the problem of "falsebeards" (Dawkins 1982; Gardner and West 2010). Third, we investigate whether these two problems may be solved in analogous ways, with a focus on mutational input and assortative mating. Fourth, we explore whether population structure facilitates the evolution of female preference and male ornamentation analogously with how it is understood to facilitate the evolution of greenbeards. We illustrate each of these analyses using formal mathematical models. More generally, by developing a conceptual bridge between these two topics, we are able to import results from the field of kin selection to sexual selection, and vice versa, yielding new insights into both areas of evolutionary biology.

Results and Discussion
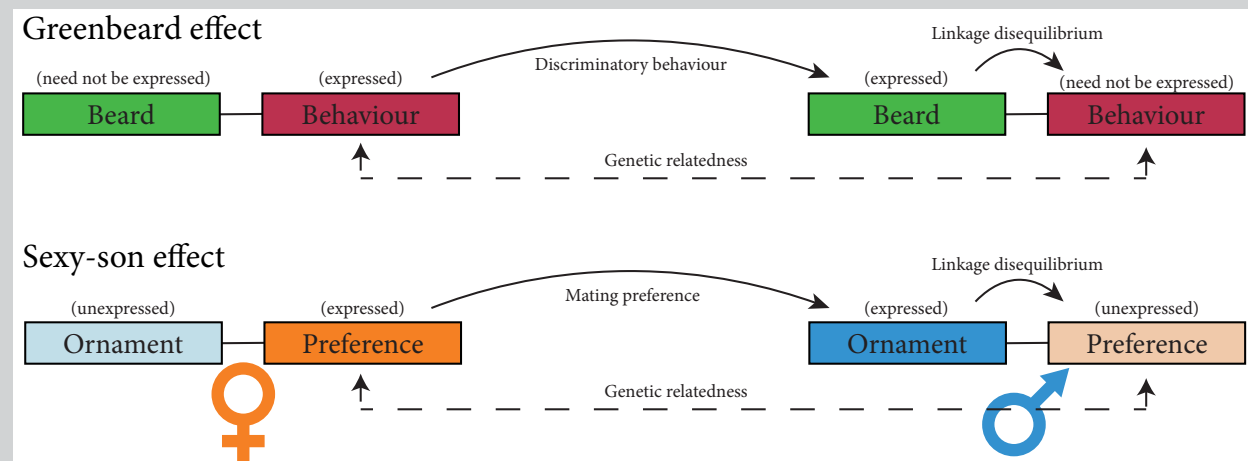### WHAT KIND OF GREENBEARD IS INVOLVED IN THE SEXY-SON EFFECT?

Gardner and West (2010) suggested that greenbeards fall into four broad categories, classified according to whether they involve helping or harming behavior, and whether this behavior is facultative or obligate: facultative-helping greenbeards enact helping behavior toward fellow greenbeards but not toward nongreenbeards; facultative-harming greenbeards enact harming behavior toward nongreenbeards but not toward fellow greenbeards; obligate-helping greenbeards enact helping behavior toward all social partners, but only fellow greenbeards are able to benefit from this; and obligate-harming greenbeards enact harming behavior toward all social partners, but only nongreenbeards are vulnerable to its deleterious effects. Note that, as average relative fitness is conserved in the population, it is impossible to improve the relative fitness of one social partner without reducing the relative fitness of others and so, to provide a meaningful distinction, helping versus harming is decided according to the "primary" effects of the greenbeard's behavior, and not according to "secondary," competitive consequences for fitness (cf. West and Gardner 2010).

BOX 1: What are greenbeard and sexy-son effects?

The term "kin selection" (Maynard Smith 1964) implies a process that occurs only in relation to social partners that are genealogically related. However, Hamilton (1964) suggested that kin selection effects may occur even in the absence of any genealogical relationship, so long as social partners share alleles in common, for whatever reason this may be. To illustrate this point, he imagined a scenario in which an allele leads its carriers to both exhibit a conspicuous phenotype–such that they may recognise each other–and also behave preferentially toward each other. Dawkins (1976) later made the illustration more vivid by imagining an allele that causes its carriers to both grow a green beard and also behave altruistically toward their green-bearded social partners, and this is the origin of the term "greenbeard effect." By showing that discriminatory altruism of this form may be favored by kin selection, Hamilton (1964) demonstrated that what is crucial is genetic relatedness *per se*, with respect to the loci that underpin social behavior, rather than genealogical relationship. Although generally described in terms of only one locus controlling both the recognition mechanism and the social behavior, the greenbeard effect also operates when these different aspects are controlled by different loci, so long as they are in linkage disequilibrium (i.e., there is a statistical association between these two loci). Typically, the assumption is that both the actor and recipient in the greenbeard interaction express both their beard and behavior alleles, in a symmetrical way, but the logic also holds for scenarios where individuals of one class express only the beard and individuals of a separate class express only the behavior (Gardner and West 2010; Biernaskie et al. 2011).

The sexy-son effect, described by Fisher (1915, 1930), provides an explanation as to why in many species females prefer to mate with males who exhibit conspicuous–and often cumbersome–ornamentation and, consequently, why males are favored to exhibit such ornamentation. A classic example is the peacock's tail, which renders the bearer more vulnerable to predation but provides improved mating success (Darwin 1871). Fisher's key insight is that if female preference for male ornamentation appears for any reason, it may be maintained by natural selection simply because any female who mates with an unornamented male runs the risk of his alleles being passed onto her sons who, being unornamented, may struggle to achieve mating success. This became known as the "sexy-son effect" when Weatherhead and Robertson (1979)–apparently independently–came up with the very same idea. Fisher suggested that the cumulative action of this sexy-son effect would lead to a "runaway process" wherein both female preference and male ornamentation may become greatly exaggerated, becoming a major hindrance to individual survival. Although usually framed in terms of individuals of different classes expressing preference and ornamentation phenotypes, the sexy-son effect does readily apply to scenarios where the very same individual may express both traits–as, for example, in hermaphrodites (Morgan 1994).

If females vary in their preference, and males in their ornamentation, then the resulting assortative mating ensures that the loci underpinning female preference and ornamentation will be in linkage disequilibrium. Accordingly, an alternative–but exactly equivalent–way of describing the sexy-son effect is that, when a female carrier of the preference allele mates with an ornamented male, she is likely providing a fitness benefit to a carrier of the same allele. This is the sense in which Fisher's sexy-son effect may be seen as a kind of greenbeard effect. Hamilton (1964) noted the possible connection between assortative mating and the greenbeard effect, but did not discuss the sexy-son effect directly. Dawkins (1986) appears to have been the first to do so, and his verbal treatment (see also Pizzari and Gardner 2012) provides the starting point for the present analysis.

This raises the question: if the sexy-son effect is a kind of greenbeard effect, then which of these four kinds of greenbeard is involved? With regard to the distinction between facultative versus obligate greenbeards, Gardner and West's (2010) classification emphasizes scenarios where actors either directly discriminate the greenbeard status of their social partners and adjust their behavior accordingly (facultative), or else constitutively express a phenotype that has different fitness consequences for fellow greenbeard versus nongreenbeard social partners (obligate). Accordingly, if the behavior that increases a female's receptiveness to matings by ornamented males–or decreases a female's receptiveness to matings by unornamented males–is activated only in the presence of such males, then the sexy-son greenbeard is of the facultative variety. In contrast, if the behavior is always expressed, irrespective

of whether the appropriate males are present and hence affected by it, then the sexy-son greenbeard is of the obligate variety. More generally, the degree to which the behavior is expressed may vary as a function of the frequency of encounters with each type of male, but not disappear completely when the corresponding male type is absent, in which case the sexy-son greenbeard may involve a mixture of facultative and obligate effects.

Most existing mathematical models of the sexy-son effect appear to implicitly assume obligate female preference (Lande 1981; Kirkpatrick 1982; Bulmer 1989; Pomiankowski et al. 1991; Day 2000; Hall et al. 2000; Bailey and Moore 2012; Kuijper et al. 2012). In particular, while they often do not spell out the mechanism by which a female's preference for ornamented males is exerted, the cost of female preference is typically assumed to be fixed and not varying as a function of the frequency of her encounters with such males (Lande 1981; Kirkpatrick 1982; Bulmer 1989; Pomiankowski et al. 1991; Day 2000; Hall et al. 2000; Bailey and Moore 2012; Kuijper et al. 2012). Notable exceptions are the models of Pomiankowski (1988) and Kokko et al. (2015), in which the cost of female preference is explicitly assumed to decrease as the frequency of ornamented males increases, implying facultative female preference. More generally, a mixture of facultative and obligate effects will often be more realistic, as some of the costs of female preference (e.g., the hazards of rejecting unwanted mating attempts) are likely to vary as a function of the rate of encounters with ornamented versus unornamented males, whereas others (e.g., overhead investment into requisite cognitive machinery) are likely to remain relatively constant.

With regards to the distinction between helping versus harming, if a female's preference is exerted by increasing her receptiveness to matings by ornamented males (e.g., proactively seeking them out) but without reducing her receptiveness to matings by unornamented males, then she may be regarded as providing help to ornamented males, and hence the sexy-son greenbeard is of the helping variety. In contrast, if she exerts her preference by reducing her receptiveness to matings by unornamented males (e.g., rejecting mating attempts) but without increasing her receptiveness to matings by ornamented males, then she may be regarded as inflicting harm upon unornamented males, and hence the sexy-son greenbeard is of the harming variety. In other scenarios–particularly where it is not possible to distinguish primary versus secondary recipients of the female's preference behavior–the sexy-son greenbeard may be viewed as involving a mixture of both helping and harming effects.

Most theoretical analyses of the sexy-son effect (Lande 1981; Kirkpatrick 1982; Bulmer 1989; Pomiankowski et al. 1991; Day 2000; Hall et al. 2000; Bailey and Moore 2012; Kuijper et al. 2012) have modeled female preference in terms of competitive outcomes–i.e., what proportion of offspring are fathered by ornamented versus unornam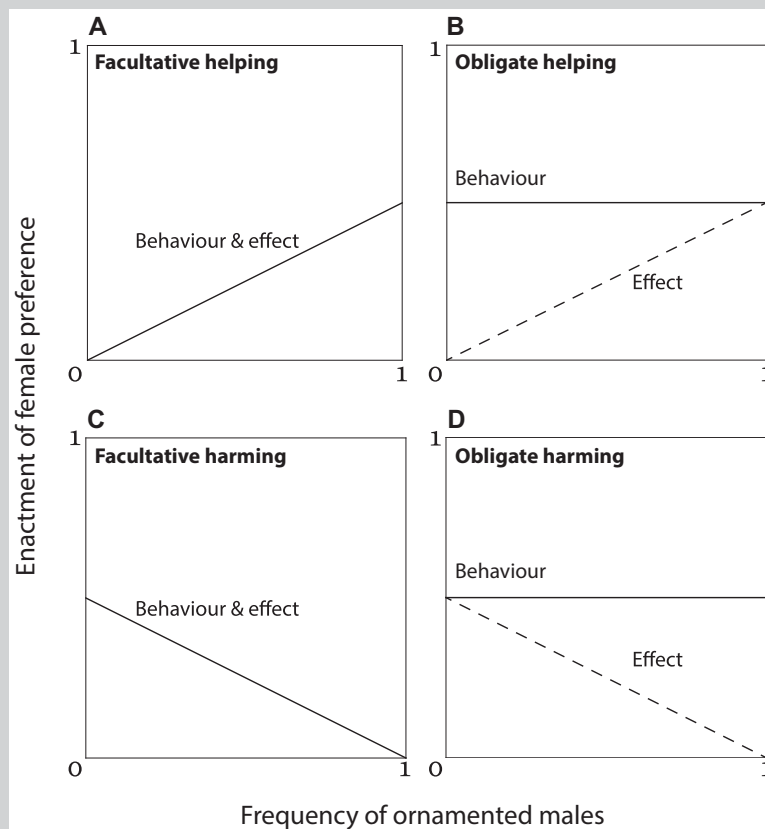ented males–without being explicit as to the particular mechanisms underpinning these outcomes. Accordingly, those models cannot be readily classified as either helping or harming. Yet the distinction is biologically meaningful: for example, if female preference were to drive male ornamentation to fixation, then while the effects of helping would continue to be observed (e.g., females would continue to be proactive in mating with ornamented males; Box 2, panels A and B), the effects of harming would vanish (e.g., there would be no unornamented males for females to actively reject; Box 2, panels C and D). That is, female preference need not simply be a case of choosing how a fixed number of matings are distributed across potential mates, but it may also modulate total number of matings and involve specific mating behaviors that would not otherwise be expressed. The models of Pomiankowski (1988) and Kokko et al. (2015) are, again, exceptional in this respect: they explicitly assume that female preference is exerted by rejection of unornamented males, and hence describe greenbeards of the harming variety. To our knowledge, no model of the sexy-son hypothesis has yet been developed that takes an explicitly helping approach, such that preference is exerted by choosy females being just as receptive to unornamented males as are nonchoosy females, but being more receptive to ornamented males than are nonchoosy females. This could potentially provide an explanation for polyandry, with already-mated females engaging in additional matings when they encounter more-highly preferred males (see Bocedi and Reid 2015 as another connection between sexy-son effect and polyandry).

IS THE SEXY-SON EFFECT RESISTANT TO FALSEBEARDS?

Pizzari and Gardner (2012) suggested that the sexy-son hypothesis may involve a special kind of greenbeard effect that is relatively resistant to falsebeards. Falsebeards are genotypes that make their carriers exhibit the phenotypic marker–i.e., the beard–that elicits the discriminatory behavior, but without expressing the discriminatory behavior itself (Dawkins 1982; Gardner and West 2010). As they accrue the benefit enjoyed by bearded individuals without paying the cost associated with the behavior, then –all else being equal–they are expected to have an evolutionary advantage over greenbeard genotypes and displace them from the population (Dawkins 1982; Gardner and West 2010; Box 3, panel A, see electronic supplementary material §1 for details). More precisely, the problem of falsebeards is characterized by a breakdown in the crucial linkage disequilibrium between beard and behavior loci that drives the greenbeard effect (Box 1; Box 3, panel A, see electronic supplementary material §1 for details), and Pizarri and Gardner (2012) suggested that this breakdown need not occur in the context of the sexy-son hypothesis as preferential mating between females carrying preference alleles and males carrying ornamentation alleles acts to continually regenerate linkage disequilibrium.

BOX 2: Female preference behaviors and their effects vary as a function of the population frequency of ornamented males

Here, we introduce a classification for sexy-son effects based on the classification used for greenbeard effects. Accordingly, and as with the greenbeard effect, four different scenarios can be described based on the particular patterns of the behavior and its effects: "Facultative helping" scenarios (panel A, below), in which females express positive-preference behavior (i.e., proactively seeking matings) only in the presence of ornamented males, with the behavior being observed more frequently as ornamentation become more frequent in the population; "Obligate helping" scenarios (panel B, below), in which females express positive-preference behavior even in the absence of ornamented males, with no change in the level of this behavior as ornamentation increases in frequency, but with an increase in the incidence of males benefiting from the behavior; "Facultative harming" scenarios (panel C, below), in which females express negative-preference behavior (i.e., actively opposing mating attempts) only in the presence of unornamented males, with this behavior being observed less frequently as ornamentation becomes more frequent in the population; and "Obligate harming" scenarios (panel D, below), in which females express negative-preference behavior even in the absence of unornamented males, with no change in the level of this behavior as ornamentation increases in frequency, but with a decrease in the incidence of males being disadvantaged by this behavior.

Pizzari and Gardner's (2012) logic implies that incorporating assortative mating into a two-locus model of the greenbeard effect should confer resistance against falsebeards. While this is indeed the case in the short term, such that the frequency of greenbeard individuals increases to a level that is greater than that attained in the absence of assortative mating (Box 3, panel C, see electronic supplementary material §1 for details), in the longer term both beard and behavior alleles disappear from the population if they incur any cost (Box 3, panel C, see electronic supplementary material §1 for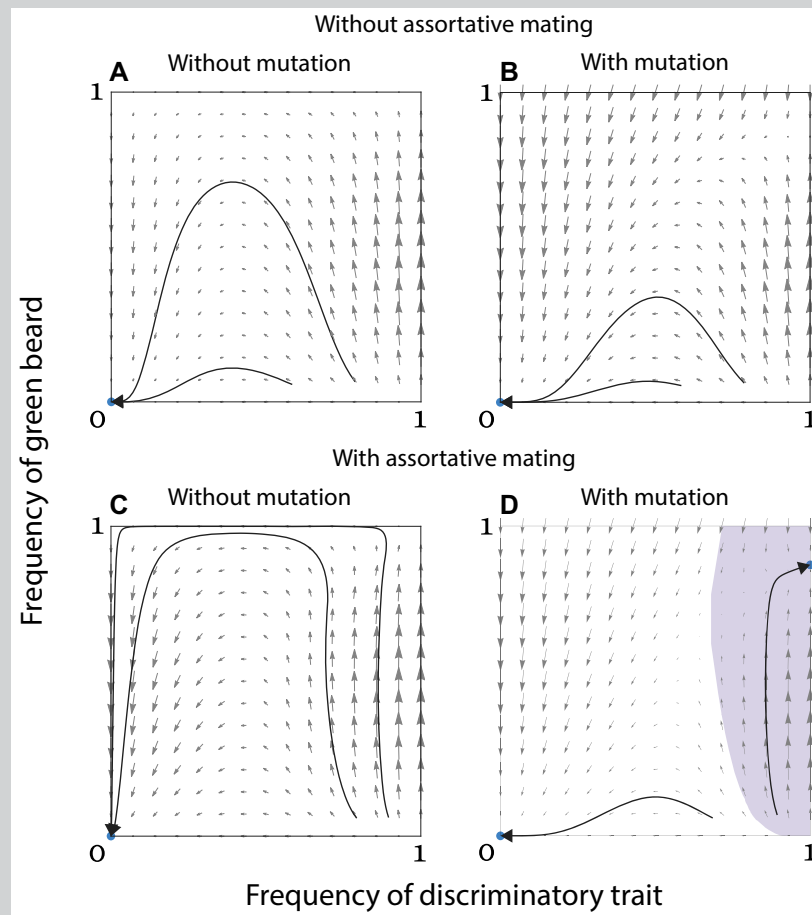 details). This is because selection for the beard phenotype erodes genetic variation at the beard locus, which makes the discriminatory behavior irrelevant (though still costly), and consequently falsebeard individuals who carry the beard allele without carrying the costly discriminatory-behavior allele are ultimately favored by natural selection. Put another way, since linkage disequilibrium between two loci can only occur when there is segregating variation at both loci, the absence of nonbearded individuals means that the crucial linkage disequilibrium between beard and behavior loci vanishes, disabling the greenbeard effect.

BOX 3: Solving the problem of falsebeards

Here, we investigate the problem of falsebeards, using obligate-harming greenbeards as an illustration (the other kinds of greenbeards are considered in the electronic supplementary material §1, yielding similar results). Consider a population of haploid hermaphrodite individuals. Individuals form social pairs at random, with a focal individual paying a fecundity cost a if they exhibit the harming behavior, which incurs a fecundity cost d for their partner if the latter does not exhibit a beard, and with the focal individual paying a fecundity cost k if they are exhibiting a beard. Individuals then repair at random and engage in a large number of such social interactions with a large number of different partners. Next, individuals form pairs to engage in sexual reproduction as follows: we randomly split the population into two equal-sized halves, with the individuals in subpopulation 1 taking the role of the "choosers" and those in subpopulation 2 taking the role of the "chosen"; individuals that exhibit the harming behavior from subpopulation 1 are then paired at random with individuals that exhibit the beard from subpopulation 2; a fraction $1 - \phi$ of these mating pairs are then broken up, and all unpaired individuals from subpopulation 1 are paired at random with unpaired individuals from subpopulation 2. In this way, there is assortative mating (to a degree that is controlled by ϕ), but all individuals have equal mating success irrespective of their genotype (see electronic supplementary material §1 for details). With the formation of a diploid zygote, recombination occurs between the harming behavior locus and the beard locus with probability r. Finally, every copy of the bearded allele has a probability μ of mutating to the nonbeard allele. Subsequently, new haploid juveniles are born and all older individuals die, which returns the population to the beginning of the life cycle.

Genotypes where genes for both the beard and the harmful behavior are present are termed "greenbeards" and genotypes where the gene for the beard is present but the gene for the harmful behavior is not are termed "falsebeards." Thus, falsebeard genotypes accrue the benefit of carrying a beard but without paying the cost associated with the behavior, potentially leading to the destabilization of the greenbeard effect (Dawkins 1982; Gardner and West 2010; Biernaskie et al. 2011).

In the absence of a source of de novo genetic variation (e.g., zero mutation, $\mu = 0$) and also of a mechanism that builds up linkage disequilibrium between beard and behavior loci (e.g., zero assortative mating, $\phi = 0$), greenbeard genotypes are not evolutionarily stable (panel A, below). Input of de novo genetic variation ($\mu = 0.05$) alone is not sufficient to stabilize greenbeards (panel B, below). Assortative mating ($\phi = 0.75$) alone is also not sufficient to stabilize greenbeards (panel C, below). Input of de novo genetic variation ($\mu = 0.05$) acting in conjunction with assortative mating ($\phi = 0.75$) can stabilize greenbeards, such that they are indefinitely maintained at nonzero frequency in the population (with the basin of attraction (shaded) shown that leads to the stable equilibrium where both traits are present (blue dot); panel D, below). While the figure illustrated here (with $k = 0.20$; $a = 0.05$; $d = 0.50$; $r = 0.50$) represents an obligate-harming-greenbeard effect, similar dynamics (described below) are observed in other types of greenbeard effects (Figs. S1–S3; see electronic supplementary material §1 for more details).

This dynamic is the greenbeard equivalent of "Crozier's paradox" of genetic kin recognition, whereby discriminatory cooperation acts to erode variation at the very loci it uses for the assessment of genealogical relationship (Crozier 1986). In the sexual selection literature, this same dynamic manifests as the "lek paradox" (Box 4, panel A, see electronic supplementary material §2 for details), whereby female preference makes itself redundant by eliminating the very genetic variation that defines preferred versus nonpreferred males (Borgia 1979). In each of these three cases, there is no selective advantage in being discriminatory–and paying the associated cost–if there are no differences to actually discriminate.

ARE THE LEK PARADOX AND THE PROBLEM OF FALSEBEARDS SOLVED IN THE SAME WAY?

The lek paradox has received a great deal of attention in the sexual selection literature, and appears to have been resolved (Borgia 1979; Kirkpatrick and Ryan 1991; Pomiankowski et al. 1991; Day 2000; Hall et al. 2000; Kotiaho et al. 2008; Kokko et al. 2015). In particular, female preference for ornamented males is prevented from becoming redundant if there is a source of de novo genetic variation that prevents the fixation of male-ornamentation, and the consequent continued selection for female preference allows the continued maintenance of ornamented males in the population (Pomiankowski et al. 1991; Day 2000; Hall et al. 2000; Kokko et al. 2015; Box 4, panel B, see electronic supplementary material §2 for details).

The similarity between the lek paradox and the problem of falsebeards suggests that introducing a source of de novo genetic variation with respect to the beard phenotype in the context of the greenbeard effect might also resolve the longstanding problem of falsebeards. Yet the introduction of new genetic variation–e.g., by spontaneous mutation–is generally associated with a breakdown of linkage disequilibrium, and so can actually exacerbate rather than resolve the problem of falsebeards (Box 3, panel B, see electronic supplementary material §1 for details). However, if the input of de novo genetic variation occurs in conjunction with assortative mating, then the former can ensure that the crucial linkage disequilibrium between beard and behavior is possible, while the latter can ensure that the crucial linkage disequilbrium is actually generated. Accordingly, the simultaneous action of both assortative mating and input of de novo genetic variation with respect to the beard phenotype can ensure the continued operation of the greenbeard effect, providing a novel solution to the longstanding problem of falsebeards (Box 3, panel D, see electronic supplementary material §1 for details).

DOES POPULATION STRUCTURE FACILITATE THE SEXY-SON EFFECT?

A hallmark of the greenbeard effect is positive frequency dependence, with bearded individuals often being favored by natural selection only if the frequency of the discriminatory behavior exceeds a certain threshold (Gardner and West 2010). This means that beard and behavior alleles may struggle to invade from rarity, which poses a significant barrier to the evolution of greenbeard phenotypes (Box 3, panel D, see electronic supplementary material §1 for details). However, Gardner and West (2010) pointed out that population structure can provide a means for overcoming this problem, as random drift may enable the alleles to reach sufficiently high frequency in a local population that they become selectively favored and subsequently spread to other parts of the wider population (Box 5, panel A, see electronic supplementary material §4 for details). Population structure leads to social partners being related via shared genealogy and not just via the greenbeard effect, but Gardner and West (2010) showed that invasion from rarity owes to the action of the greenbeard mechanism rather than a simple consequence of population structure modulating genealogical relationship.

The sexy-son effect also exhibits this same positive frequency dependence, with male ornamentation alleles being favored only when female preference exceeds a threshold level, and female preference alleles being favored only when ornamented males are encountered sufficiently often (Box 4, panel B, see electronic supplementary material §2 for details). Accordingly, male preference and female ornamentation alleles may struggle to invade from rarity, which poses a significant barrier for the sexy-son effect. The similarity of greenbeard and sexy-son effects suggests that population structure might facilitate the latter in much the same way as it has been shown to facilitate the former. Indeed, female preference and male ornamentation alleles can drift to sufficiently high frequency in the local population that they become selectively favored and are able to spread to other parts of the wider population, such that they are able to invade populations from vanishingly low global frequencies (Box 5, panel B, see electronic supplementary material §5 for details).

Previously, mathematical models of the sexy-son effect have assumed well-mixed populations, and have accordingly suffered from the problem that female preference and/or male ornamentation alleles must be initially at reasonably high frequency in order for their coevolution to get started (Lande 1981; Kirkpatrick 1982; Pomiankowski 1988; Bulmer 1989; Kokko et al. 2015). To our knowledge, the only previous model of the sexy-son effect to incorporate population structure is that of Day (2000), but this model renders the invasibility problem moot by artificially assuming a positive, constant genetic association between female
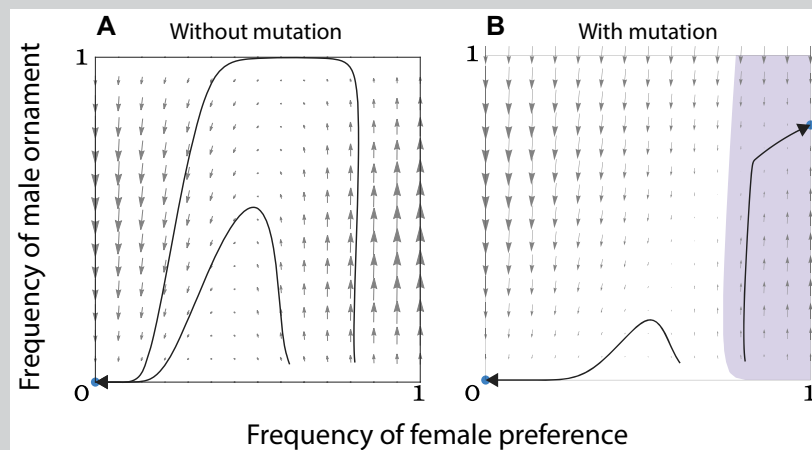
preference and male ornamentation from the outset (Holman and Kokko 2014 also consider the role of population structure in maintaining female preference, but not in the context of the sexy-son effect). Other theoretical contributions on the topic of the sexy-son effect have explicitly or implicitly assumed that female preference and/or male ornamentation have already attained high frequency for reasons not connected with the sexy-son effect (Fisher 1915, 1930; Lande 1981; Kirkpatrick 1982; Pomiankowski 1988;

Bulmer 1989; Kokko et al. 2015). This neglect of population structure appears to be driven by a traditional focus on charismatic megafauna, such as peacocks, for which the absence of population structure may be a reasonable assumption. However, many animal species–including numerous small, wingless arthropods, such as bed bugs (Vargo et al. 2011)–are characterized by significant population structure, and these may represent avenues for renewed empirical investigation on the sexy-son effect.

BOX 4: Solving the problem of lek paradox

Here, we investigate the lek paradox, with a focus on the sexy-son effect when the female preference cost is not dependent on the frequency of ornamented males for illustration (other kinds of sexy-son effects are considered in the electronic supplementary material §2, yielding similar results). Consider a population of haploid individuals separated into an equal number of males and females. Females pair up with a male according to their sexual preferences: nonchoosy females select a male at random, while choosy females preferred to pair with an ornamented male by a factor of α (with $\alpha = 0$ being random mating and $\alpha = 1$ full preference for ornamented males) but incur a fecundity cost ψ by manifesting such preference. Males pay a fecundity cost κ if they exhibit the ornament, but this makes them being preferred by the choosy females. After the sexual interactions, diploid zygotes are formed and recombination occurs between the female preference locus and the male ornament locus with probability r. Finally, every copy of the ornamented allele has a probability μ of mutating to the nonornamented allele. After this, new haploid juveniles are born, and all older individuals die, and this returns the population to the beginning of the life cycle.
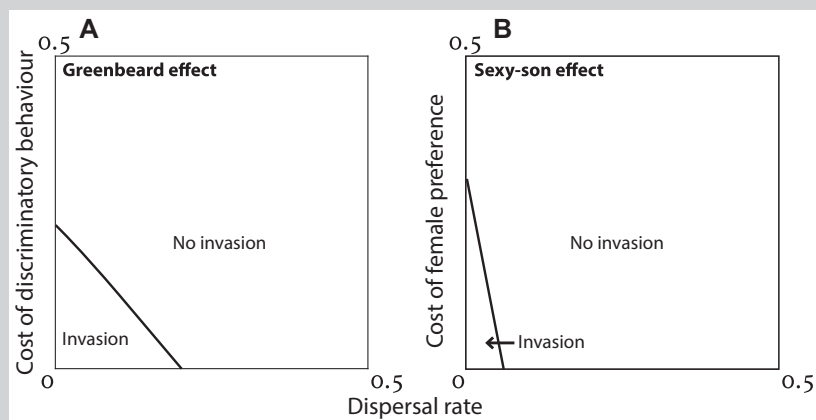
It has been long recognized that, in absence of any other stabilizing processes, the sexy-son effect may be unstable due to the increase of genotypes that carry the ornamentation allele but not the female preference allele–this has been called the "lek paradox" (Borgia 1979). In the absence of a source of de novo genetic variation (e.g., zero mutation, $\mu = 0$), female preference and male ornamentation genotypes are not evolutionarily stable (panel A, below). Input of de novo genetic variation ($\mu = 0.05$) can stabilize female preference and male ornamentation, such that they are indefinitely maintained at nonzero frequency in the population (with a basin of attraction (shaded) that leads to the stable equilibrium (blue dot); panel B, below). While the figure illustrated here (with $\alpha = 0.50$, $\psi = 0.03$, $\kappa = 0.40$, and $r = 0.50$) represents a sexy-son effect with the female preference cost not dependent on the frequency of ornamented males, the same general dynamics (described below) are present when the cost is frequency-dependent (Figs. S4–S5; see electronic supplementary material §2 for more details).

BOX 5: Population structure enables invasion of greenbeard and sexy-son alleles

In the context of the greenbeard effect, beard and behavior alleles may struggle to invade from rarity in well-mixed populations (full dispersal, see Box 3) but may be able to invade more readily in structured populations with limited dispersal m, so long as the cost of the behavior a is sufficiently small (Gardner and West 2010). Therefore, if the greenbeard-effect model described in Box 3 has its population divided into patches where social and sexual interactions occur, the greenbeard phenotypes can now evolve from rarity (panel A, below, with cost of being harmed $d = 0.75$, cost of beard $k = 0.10$, assortative mating $\phi = 0.75$, recombination rate $r = 0.50$; see electronic supplementary material §4 and Fig. S6 for more details).

In the context of the sexy-son effect, female preference and male ornament alleles may also struggle to invade from rarity in well-mixed populations (full dispersal, see Box 4) but may be able to invade more readily in structured populations. Therefore, if the sexy-son-effect model described in Box 4 has its population divided into patches where sexual interactions occur, both the female preference and the male ornament phenotypes can now evolve from rarity, as long as there is limited female dispersal m_f and the cost of the female preference ψ is sufficiently small (panel B, below, with female preference $\alpha = 0.75$, cost of ornament $\kappa = 0.10$, dependency on the frequency of ornamented males $f = 0$, rate of recombination $r = 0.50$, rate of male dispersal $m_m = 0.50$; see electronic supplementary material §5 and Fig. S7 for more details).

Conclusion

We have formally investigated the suggestion of Pizzari and Gardner (2012) that the sexy-son effect can be viewed as a greenbeard effect. Specifically, we have: (1) asked what kind of greenbeard effect is involved in the sexy-son effect, revealing that this depends on biological considerations that have previously been neglected in models of sexual selection; (2) explored the similarities between the problem of falsebeards and the lek paradox, in terms of the erosion of genetic diversity with respect to a discriminated trait undermining selection for discrimination itself; (3) shown that, in analogy with how the lek paradox has been solved by invoking factors that generate new variation (such as spontaneous mutation), these same factors may also provide a solution to the problem of falsebeards; (4) pointed out that while both greenbeard and sexy-son effects may struggle to become initially established, owing to positive frequency-dependent selection, both effects may be promoted by population structure, a factor that has previously been explored in the greenbeard literature but has been neglected by existing models of the sexy-son effect. Thus,

by building a conceptual bridge between these two evolutionary topics, we have been able to import insights from each literature to the other, yielding new solutions to longstanding problems.

Connecting the concepts of greenbeard and sexy-son effects suggests a range of avenues for future theoretical and empirical exploration. Our focus has been on individual-level adaptation, but the greenbeard effect has long been implicated in gene-level adaptation and intragenomic conflict (Alexander and Borgia 1978; Ridley and Grafen 1981; Biernaskie et al. 2011; Farrell et al. 2015), suggesting that the sexy-son effect might also be usefully investigated from an intragenomic conflict perspective. Specifically, Biernaskie et al. (2011; see also Gardner and Úbeda 2017) have identified greenbeard-related intragenomic conflict as arising in the context of a structured population where there is interaction with genealogical kin, and although population structure has previously been neglected by models of the sexy-son effect our analysis has suggested that it may be an important driver of the sexy-son effect. Also, while our focus has been on genetically encoded phenotypes, the basic logic of the greenbeard and sexy-son effects appears to hold for culturally transmitted phenotypes.

For example, socially learned female preference may account for an apparent lack of linkage disequilibrium between preference and ornamentation loci in empirical studies that have looked for it (Bailey and Moore 2012; Prokop et al. 2012; Greenfield et al. 2014; Varela et al. 2018). However, the quantitative consequences of cultural versus genetical inheritance for greenbeard and sexy-son effects remain to be investigated.

AUTHOR CONTRIBUTIONS
G. S. F., S. A. M. V., and A. G. designed the study, G. S. F. led the theoretical analysis, and G. S. F., S. A. M. V., and A. G. wrote the article.

DATA ARCHIVING
The appendix with details of the mathematical model is provided in the ESM.

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Supporting Information
Additional supporting information may be found online in the Supporting Information section at the end of the article:

Table S1. Payoffs to type X individuals for interacting with type Y individuals (possible types: neutral N, falsebeard F, helper/harmer H, and greenbeard G).
Table S2. The frequencies of the different mating types for a greenbeard-effect model where assortative mating is possible.
Figure S1. Solving the problem of falsebeards in a facultative-helping greenbeard effect.
Figure S2. Solving the problem of falsebeards in an obligate-helping greenbeard effect.
Figure S3. Solving the problem of falsebeards in a facultative-harming greenbeard effect.
Figure S4. Solving the lek paradox in a sexy-son effect with increased frequency-dependent female preference cost.
Figure S5. Solving the lek paradox in a sexy-son effect with decreased frequency-dependent female preference cost.
Figure S6. Population structure enables invasion of facultative helping greenbeards (A), of obligate helping greenbeards (B), of facultative harming greenbeards (C), and of obligate harming greenbeards (D).
Figure S7. Population structure enables invasion of a sexy-son effect with increased frequency-dependent female preference cost (A), of a sexy-son effect with decreased frequency-dependent female preference cost (B), and of a sexy-son effect with frequency-independent female preference cost (C).