Unbalanced selection: the challenge of maintaining a social polymorphism when a supergene is selfish

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1 **Abstract**

2 Supergenes often have multiple phenotypic effects, including unexpected detrimental ones, because

3 recombination suppression maintains associations among co-adapted alleles but also allows the

4 accumulation of recessive deleterious mutations and selfish genetic elements. Yet, supergenes often persist

5 over long evolutionary periods. How are such polymorphisms maintained in the face of selection, drive

6 and drift? We present a population genetic model that investigates the conditions necessary for a stable

7 polymorphic equilibrium when one of the supergene haplotypes is a selfish genetic element. The model

8 fits the characteristics of the Alpine silver ant, *Formica selysi*, in which a large supergene underlies colony

9 social organization and one haplotype distorts Mendelian transmsission by killing progeny that did not

10 inherit it. The model shows that such maternal-effect killing strongly limits the maintenance of the social

11 polymorphism. Under random mating, transmission ratio distortion prevents rare single-queen colonies

12 from invading populations of multiple-queen colonies, regardless of the fitness of each genotype. A stable

13 polymorphic equilibrium can, however, be reached when high rates of assortative mating are combined

14 with large fitness differences among supergene genotypes. The model reveals that the persistence of the

15 social polymorphism is non-trivial and expected to occur only under restrictive conditions that deserve

16 further empirical investigation.

Introduction

18 Supergenes – large non-recombining genomic regions – underlie some of the more striking

19 polymorphisms in nature [1, 2]. They commonly affect multiple traits of the phenotype, controlled by

20 linked alleles, of which some are co-adaped [3, 4]. Supergenes are also prone to accumulate recessive

21 deleterious mutations [2, 5] and selfish genetic elements that distort the laws of Mendelian inheritance

22 [6-8]. Indeed, the lack of recombination hinders the purging of deleterious elements and allows the

23 accumulation of selfish genetic elements that favour their own transmission, such as toxin-antidote

24 elements [9]. Yet, supergenes often persist over long evolutionary periods [10]. How are such

25 polymorphisms balanced in the face of selection, drive, and drift? Fundamental mechanisms leading to

26 balanced polymorphisms at supergenes include various forms of negative frequency-dependent

27 selection, temporally or spatially-varying selection, and overdominance [2, 5]. Because supergenes have

28 complex effects, understanding their evolutionary trajectory remains a substantial challenge.

29 A supergene usually arises when recombination is suppressed, often as a result of an inversion, so that a

30 group of neighbouring genes becomes inherited as a single Mendelian element. The long-term fate of the

31 novel haplotype will depend on drift and on the combined selective effects over multiple supergene

32 elements. A mutant non-recombining haplotype will spread if it has captured adaptive combinations of

33 alleles [the supergene hypothesis; reviewed in 4]. Non-recombining haplotypes can also spread selfishly,

34 by being transmitted to a disproportionate number of adult offspring. Indeed, gene drive arises when a

35 driver locus (typically with toxic "killer" effects on the product of a responder locus) becomes tightly

36 linked to an insensitive allele at the responder locus, so that the selfish genetic elements is not suicidal

37 [6, 9]. Such selfish genetic elements tend to be located in non-recombining regions, like supergenes [8,

38 11]. Counteracting these advantages, non-recombining haplotypes are predicted to accumulate

39 deleterious mutations [5]. Hence, in many cases homozygous lethality prevents a positively selected or

40 driven haplotype from reaching fixation [1, 2]. As supergenes influence multiple traits at once, which

41 often have confounding or antagonistic effects, formal modelling is needed to understand their

42 evolutionary dynamics.

43 Here, we present a model examining the conditions for the long-term persistence of a polymorphism in a

44 supergene controlling alternative forms of social organisation in ants, in which one haplotype is a

45 transmission ratio distorter. The model is designed to fit the properties of the Alpine silver ant, *Formica*

46 *selysi*. This species is polymorphic for colony social organisation: within the same populations, it forms

47 monogynous colonies, which have a single reproductive queen, and polygynous colonies, in which

multiple queens share offspring production [12-14]. A genome-wide association study coupled with linkage maps has identified that a large supergene with two highly differentiated non-recombining haplotypes, *Sm* and *Sp*, underlies this social polymorphism [15]. We will simplify the notation slightly and refer to the *Sm* haplotype as *M* and the *Sp* haplotype as *P*. Mature (= large-sized, several years old) monogynous colonies consist of individuals carrying exclusively the *M* haplotype: all females (queens and workers) have the supergene genotype *MM*, while all males have the haplotype *M* (females are diploid and males haploid in ants; Figure 1a). In contrast, polygynous colonies consist of female ants carrying at least one copy of the *P* haplotype, i.e. having the supergene genotype *PP* or *MP*, and producing only *P* males (Figure 1b). Monogynous colonies are established by *MM* queens independently, without the help of workers, whereas polygynous colonies are founded by *MP* or *PP* queens, and possibly *MM* queens mated to *P* males, either independently or accompanied by workers from their natal colony (Figure 1).
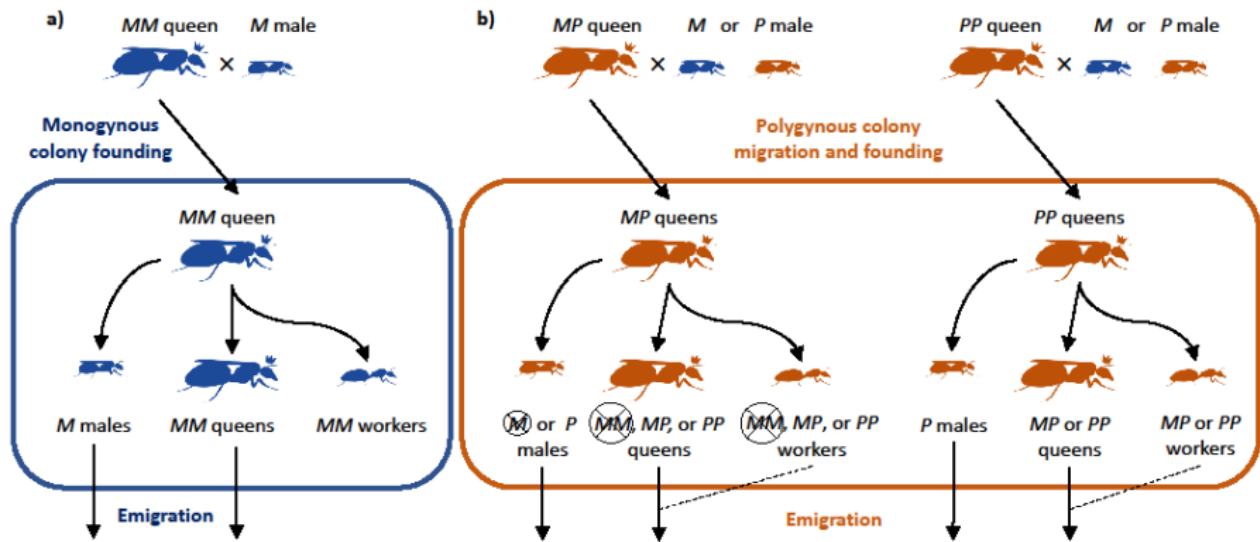
Figure 1. Social and genetic system of *F. selysi*. (a) Mature monogynous colonies contain a single *MM* queen mated with an *M* male. The queen produces *M* males (haploid, from unfertilized eggs), as well as *MM* queens and *MM* workers (diploid, from fertilized eggs). The offspring (males and queens) fly out of the colony for mating, and queens establish colonies independently. (b) Mature polygynous colonies contain multiple *MP* or *PP* queens mated with either *M* or *P* males. The offspring (queens and males) also fly out of the colony for mating. *MP* and *PP* queens (and possibly *MM* queens mated to *P* males) may establish colonies independently, or, for polygynous queens, with the help of workers from their natal colony (dashed line). The *P* haplotype acts as a maternal effect killer, so that all offspring of *MP* queens that do not inherit the *P* haplotype die during development. As a result, *M* males and *MM* females are never produced by polygynous colonies.

The supergene controlling social organization in *F. selysi* is very ancient, being shared by multiple *Formica* lineages separated by 20-40 MY of independent evolution [16]. The two haplotypes have accumulated substantial sequence divergence and differ by several inversions [15, 16]. Field data in *F.*

selysi suggest that the proportion of monogynous and polygynous colonies tends to be stable across years, remaining close to 50% in one well-studied population [12, 14], while varying between patches of mosaic habitat within populations [17]. Moreover, many populations contain both types of colonies [18]. Overall, the comparative genomic and population genetic data show the signature of strong and persistent balancing selection, consistent with an evolutionarily stable polymorphism.

Genetic and behavioral data indicate ongoing gene flow between the monogynous and polygynous social forms of F. selysi. First, the two social forms show no or minimal signs of genetic differentiation across most of their genome, outside of the supergene [15, 19]. Second, monogynous and polygynous colonies are found in close spatial proximity within the same populations [12, 17, 18]. Third, virgin queens and males fly to mating sites on neighbouring trees, where they mate [12, 20]. Queens and males from alternative social forms readily mate in choice experiments [21], as well as in field mating swarms [20]. In mature field colonies, the polygynous queens had frequently mated with males of monogynous origin, whereas the monogynous queens had only mated with males of monogynous origin, which suggests unidirectional gene flow from the monogynous to the polygynous social form [19]. However, recent analyses of mating swarms and incipient colonies revealed that MM females do mate with P males [20, 22]. These queens might establish colonies that do no reach a mature size or that become polygynous, given that in the field, we never detected a mature colony headed by a single monogynous queen mated with a P male [15, 19].

Mating in Alpine silver ants is non-random with respect to the social form of queens and males [15, 19, 20]. The sampling and genotyping of ants from mature field colonies revealed that queens from monogynous colonies had mated exclusively with M males (n = 69 matings), while queens from polygynous colonies had mated with both P and M males, the latter accounting for 23% of the matings, for both MP and PP queens (n = 190 matings) [19]. While matings outside of the colony have been well documented [12, 20], evidence for within-colony mating is only indirect [19]. In monogynous colonies, mates were not significantly related to queens, suggesting that within-colony mating is rare or absent in this social form. In polygynous colonies, mates were slightly related to queens, suggesting that some of the queens had mated with nestmate males within or near the natal colony [19]. Queens occasionally mate with multiple males [12, 19]. Local mate availability or mate preferences, as well as sperm discrimination or fertility differences after mating, may influence the probability of each cross. After mating, both types of queens are able to establish colonies independently [22]. In addition, polygynous queens may establish colonies with workers from their natal colony (colony budding). Overall, due to

104   pronounced differences in life-history, including dispersal, mating and colony founding [13, 20], queens

105   from alternative social forms are likely to greatly differ in fitness.

106   A striking feature of the genetic system underlying this social polymorphism is that the *P* haplotype acts

107   as a maternal-effect killer, causing the early death of any offspring of *MP* mothers that do not bear the *P*

108   haplotype [8; Figure 1b]. While *MP* females commonly mate with *M* males and produce *MP* and *MM*

109   eggs in Mendelian proportions (no meiotic drive), *MM* or *M* eggs from *MP* mothers fail to hatch [8, 19].

110   Thus, *MP* females never produce adult *MM* daughters nor *M* sons (Figure 1b). In short, the *P* haplotype

111   causes complete gene drive, distorting Mendelian transmission in such a way that all offspring produced

112   by polygynous colonies carry a *P* haplotype. Furthermore, substantial fitness differences have been

113   detected among females carrying alternative genotypes, in both the lab and the field (Blacher, De

114   Gasperin, Grasso, Sarton-Lohéac, Alleman and Chapuisat, unpublished results).

115   In this article, we show that the transmission ratio distortion induced by maternal-effect killing strongly

116   limits the maintenance of the social polymorphism. We develop a population genetic model that

117   incorporates the known aspects of the genetic, social, and mating systems of *F. selysi*. Using this model,

118   we determine the conditions necessary to reach a stable polymorphic equilibrium. Our model reveals

119   that, under many conditions, classical forms of balancing selection, including when selfish genetic

120   elements are balanced by strong counterselection in homozygotes, fail to stabilize the social

121   polymorphism. In other examples of transmission ratio distortion (e.g., tailless in mice), an element that

122   is driven (e.g., the *t* allele) spreads when rare but is prevented from fixing by the sterility of *tt* males

123   [23]. With *F. selysi*, however, maternal-effect killing prevents *MP* females from producing the *MM*

124   females that are needed to establish monogynous colonies. Thus, while low fitness of the driven

125   haplotype *P* can ensure that *M* spreads when rare, the result is generally an equilibrium consisting of

126   only *PP* and *MP* females in polygynous colonies, and the social polymorphism is lost. Even if maternal-

127   effect killing is not complete and the occasional *M* son or *MM* daughter is produced, they would

128   generally fail to establish new monogynous colonies, because most of their matings would be with

129   polygynous individuals, whose offspring are of the polygynous type. Hence, when mating is random,

130   maternal effect killing leads to the extinction of monogynous colonies regardless of how strong selection

131   is against homozygotes. Overall, as we will show, the gene drive caused by maternal-effect killing

132   destabilizes the genetic polymorphism and precludes the maintenance of a social polymorphism with

133   both polygynous and monogynous colonies when mating is random and fitnesses are frequency-

134 independent. The goal of this paper is to determine what exactly could account for the maintenance of
135 the supergene polymorphism and both social forms.

136 Here we briefly outline the approach that we take, section by section. We start by constructing a general
137 model that can be used to explore all scenarios described below. We then apply this model to different
138 forms of reproduction, starting with random mating, to determine the conditions under which the social
139 polymorphism observed in *F. selysi* would be stable:

140 1) Random Mating: We first considered the case of a randomly mating population, allowing for
141   arbitrarily strong natural selection, finding that the social polymorphism is never stable.
142 2) Variation in Fertility: We then include fertility differences between mating pairs, again finding
143   that the social polymorphism is never stable.
144 3) Sexual Selection: Next, we incorporate sexual selection, using the fixed relative preference
145   scheme of Kirkpatrick [24]. This model assumes that all queens will be mated and that their
146   preferences determine the relative frequency of mating with *M* and *P* males. Again, we show that
147   a social polymorphism is not maintained except when sexual selection is so extreme that it
148   results in assortative mating.
149 4) Assortative Mating: Finally, we model assortative mating, finding that partial (but not complete)
150   assortative mating can maintain the social polymorphism if combined with strong enough
151   selection.

152 Together, these models demonstrate how challenging it is to maintain the *F. selysi* social polymorphism
153 because of the selfish supergene drive of the *P* haplotype and clarify the conditions required to account
154 for the persistence of both monogynous and polygynous colonies.

155 **Model**

156 Motivated by *F. selysi*, we develop a population genetic model to investigate the conditions necessary
157 for a stable polymorphic equilibrium when one haplotype is a maternal-effect killer. This model with
158 non-overlapping generations and male-haploidy follows the dynamics of genotypes at a supergene
159 controlling social organisation among reproductive females (= queens) and among males separately
160 (Table 1). Because workers do not reproduce (Figure 1), we do not incorporate them within the
161 population dynamics, except indirectly via the fitness of queens and males. We census at the adult stage,
162 among surviving ants, who then mate and reproduce, followed by selection among their offspring (see
163 Appendix Table for definitions of all parameters).

Table 1. Genotype frequencies among adult queens and males. Social form refers to the social organization of the colony of origin.

Supergene genotype	Sex	Social form	Frequency
MM	Queen	Monogynous	X_{MM}
MP	Queen	Polygynous	X_{MP}
PP	Queen	Polygynous	X_{PP}
M	Male	Monogynous	Y_M
P	Male	Polygynous	Y_P

164   To model the production of males, which is not dependent on mating, we let $O^{\male}_{a|ij}$ represent the

165   production rate of surviving male offspring of genotype *a* produced by a queen of genotype *ij*. We

166   assume Mendelian segregation but allow the number and survival of the male offspring, $V^{\male}_{a|ij}$, to depend

167   on its mother's genotype, enabling us to incorporate maternal effects, including maternal-effect killing,

168   and effects of colony type on fitness. For example, *MP* queens at frequency X_{MP} produce *M* and *P* males

169   at rates proportional to:

$$O^{\male}_{M|MP} = \frac{1}{2} X_{MP}\, V^{\male}_{M|MP} \tag{1a}$$

$$O^{\male}_{P|MP} = \frac{1}{2} X_{MP}\, V^{\male}_{P|MP} \tag{1b}$$

172   If there is complete maternal-effect killing of all offspring that did not inherit the *P* haplotype from their

173   *MP* mother, then $V^{\male}_{M|MP} = 0$. If colonies are unable to recover the resources invested in lost males, $V^{\male}_{P|MP}$

174   is expected to be near one (all else being equal). If colonies are able to fully recover the energy invested

175   in lost embryos and use it to produce *P* males, then $V^{\male}_{P|MP}$ may be elevated relative to other male

176   fitnesses.

177   To model the production of queens, we let $O^{\female}_{ab|ij \times k}$ represent the production rate of surviving queen

178   offspring of genotype *ab* produced from matings between a queen of genotype *ij* and a male of genotype

179   *k*. As described below, $O^{\female}_{ab|ij \times k}$ incorporates both the reproductive mode and several components of

180   fitness, including the rate at which different crosses occur, fertility differences, offspring number, and

181   the survival rate of daughters, $V^{\female}_{ab|ij \times k}$ (Table 2). We assume that the zygotes are produced in a

182   Mendelian fashion but allow complete maternal-effect killing, eliminating MM offspring of MP mothers

183    $(V^{\female}_{MM|MP \times M} = 0)$.

Table 2. Production of queens

Mating	Frequency	Viability of ab offspring	Proportion of MM offspring	Proportion of MP offspring	Proportion of PP offspring
$MM \times M$	$R_{MM \times M}$	$V^{\female}_{ab|MM \times M}$	1	0	0
$MM \times P$	$R_{MM \times P}$	$V^{\female}_{ab|MM \times P}$	0	1	0
$MP \times M$	$R_{MP \times M}$	$V^{\female}_{ab|MP \times M}$	1/2	1/2	0
$MP \times P$	$R_{MP \times P}$	$V^{\female}_{ab|MP \times P}$	0	1/2	1/2
$PP \times M$	$R_{PP \times M}$	$V^{\female}_{ab|PP \times M}$	0	1	0
$PP \times P$	$R_{PP \times P}$	$V^{\female}_{ab|PP \times P}$	0	0	1

184   To model mating, we introduce an arbitrary reproductive function, $R_{ij \times k}$, that describes the frequency of

185   crosses between queens of genotype ij and males of genotype k. This function depends on the

186   reproductive mode considered in each section of the results:

       187   1) Random Mating: When mating is random, $ij \times k$ crosses occur at a frequency of $R_{ij \times k} = X_{ij}\, Y_k$.

       188   2) Variation in Fertility: If there are fertility differences among mating pairs ($f_{ij \times k}$), but mating is

       189   otherwise random, we set $R_{ij \times k} = f_{ij \times k} X_{ij}\, Y_k$, where $f_{ij \times k}$ is measured relative to the mean

       190   fertility in each generation.

       191   3) Sexual Selection: Using the fixed relative preference scheme of Kirkpatrick [24], females of

       192   genotype ij mate with each type of male k in proportion to her mating preference ($\alpha_{ij \times k}$), leading

       193   to $R_{ij \times k} = X_{ij}\, \dfrac{\alpha_{ij \times k} Y_k}{\alpha_{ij \times P} Y_P + \alpha_{ij \times M} Y_M}$, where females are assumed to be able to remate after rejecting a

       194   mate. If mating preferences are costly, this is assumed to be incorporated into the female's

       195   viability ($V^{\female}_{ab|ij \times k}$), regardless of the composition of the male population (a consititutive cost of

       196   sexual selection).

197   4)   Assortative Mating: Finally, we consider assortative mating by social type with $R_{MM \times M} =$

198        $(1 - m_M) X_{MM} Y_M + m_M X_{MM}$, where a proportion m_M of all *MM* queen mating is by assortment

199   with males from their own social form regardless of the frequency of *M* males (see equation (9)

200   for additional crosses).

201   Importantly, except with assortative mating, the frequency of matings involving rare genotypes is

202   proportional to the frequency of the rare female times the frequency of the rare male (e.g., proportional

203   to $X_{MM} Y_M$ when both *MM* females and *M* males are rare).

204   Overall, the production of *MP* queens from matings between *MP* queens and *P* males, for example, is

205   proportional to:

206
$$O^{\female}_{MP|MP \times P} = \frac{1}{2} R_{MP \times P} \, V^{\female}_{MP|MP \times P} \tag{2}$$

207   Finally, we normalize the frequencies in each sex to obtain the genotype frequencies in the next

208   generation among queens and males, respectively:

209
$$X'_{ab} = \frac{\sum_{ij,k} O^{\female}_{ab|ij \times k}}{\sum_{ab,ij,k} O^{\female}_{ab|ij \times k}} \tag{3a}$$

210
$$Y'_a = \frac{\sum_{ij} O^{\male}_{a|ij}}{\sum_{a,ij} O^{\male}_{a|ij}} \tag{3b}$$

211   where the sums in the numerator are taken over all maternal (*ij*) and, for female offspring, paternal

212   genotypes (*k*), and the sums in the denominator are also taken over all offspring genotypes (*ab* for

213   female and *a* for male offspring). Given this normalization, all fitnesses need only be measured relative

214   to one another within a sex, so we consider $V^{\male}_{a|ij}$ and $V^{\female}_{ab|ij \times k}$ to vary between 0 and 1 in our numerical

215   analysis.

216   *F. selysi* queens may differ in how they form new colonies. Queens from monogynous colonies fly away

217   from their natal colony and establish novel colonies independently, while queens from polygynous

218   colonies may also establish novel colonies with the help of workers, by walking away from their natal

219   colony [colony budding; 12, 25]. Furthermore, polygynous colonies are larger than monogynous

220   colonies, in line with their greater number of queens and longer colony lifespan [13]. Queens of

221   monogynous origin may, however, be more successful at establishing new colonies independently,

222   compared to queens of polygynous origin [21, 26]. We do not explicitly model colony dynamics but

223   include any fitness differences in colony success through the fitness terms, $V^{\male}_{a|ij}$ and $V^{\female}_{ab|ij\times k}$, which also

224   allows for the possibility that a queen's fitness depends on her parents' genotypes through their effect on

225   the colony type and the genotypes of siblings. All of the recursion equations and the full analyses are

226   detailed in the supplemental *Mathematica* file.

227   **Maintenance of the social polymorphism**

228   Below, we analytically search for conditions under which both monogynous and polygynous colonies

229   will increase when rare, indicating that there is a protected polymorphism. We assume that maternal-

230   effect killing is complete [8], with $V^{\female}_{MM|MP\times M} = V^{\male}_{M|MP} = 0$, although we discuss the effect of allowing

231   some *M* male and *MM* female offspring to be produced by *MP* mothers. We supplement this analysis

232   with numerical searches, drawing parameters at random (as specified below) and determining

233   numerically all equilibria and their stability properties. These numerical searches were used to confirm

234   the analytical results and to determine whether stable internal polymorphisms could occur even when the

235   polymorphism was not protected (i.e., when monogynous and polygynous colonies could not both

236   increase when rare).

237   *1) Random Mating* – We start by considering the case of random mating, $R_{ij\times k} = X_{ij} Y_k$. With complete

238   maternal-effect killing, there are three ways that the social polymorphism could be lost from the system

239   at equilibrium: (a) *MM* queens and *M* males are fixed, (b) *PP* queens and *P* males are fixed, and (c) *PP*

240   and *MP* queens co-exist alongside *P* males. The first of these equilibria consists only of monogynous

241   colonies, while the other two consist only of polygynous colonies, falling along the polygynous edge

242   defined by the absence of *MM* queens and *M* males ($X_{MM} = Y_M = 0$; recall that maternal-effect killing

243   prevents monogynous genotypes from being produced by the *MP* queens).

244   A local stability analysis (supplementary material) shows that, under random mating, monogynous

245   fixation with *MM* queens and *M* males is unstable to the introduction of the *P* haplotype when:

$$V^{\female}_{MM|MM\times M} V^{\male}_{M|MM} < \frac{V^{\female}_{MP|MM\times P} V^{\male}_{P|MP} + V^{\female}_{MP|MP\times M} V^{\male}_{M|MM}}{2} \tag{4}$$

11

247 This result shows that polygynous colonies can spread when rare if the P haplotype confers a higher

248 average fitness, calculated as the average fitness of offspring queens that bear the rare P haplotype when

249 the P was inherited from the father (first term in the fraction) or the mother (second term), in each case

250 multiplied by the fitness of the father.

251 Along the polygynous edge, the system equilibrates at either the fixation of PP queens and P males or an

252 equilibrium with a mixture of MP and PP queens and P males, where the equilibrium frequency of MP

253 queens is:

254
$$\hat{X}_{MP} = \frac{V^{\female}_{MP|MP \times P} - 2\, V^{\female}_{PP|PP \times P}}{V^{\female}_{MP|MP \times P} + V^{\female}_{PP|MP \times P} - 2\, V^{\female}_{PP|PP \times P}} \tag{5}$$

255 Note that equilibrium (5) is valid ($0 < \hat{X}_{MP} < 1$) only when MP queen viability is more than twice that

256 of PP queens ($V^{\female}_{MP|MP \times P} > 2\, V^{\female}_{PP|PP \times P}$). Of the two equilibria along the polygynous edge ($\hat{X}_{MP}$ equal to

257 0 or to (5)), only one is ever stable. Specifically, polygynous colonies consisting of only PP queens are

258 unstable to the introduction of MP queens if:

259
$$V^{\female}_{PP|PP \times P} < \frac{V^{\female}_{MP|MP \times P}}{2}, \tag{6}$$

260 in which case the equilibrium with only MP and PP queens (5) is stable. Conversely, if condition (6)

261 fails to hold, then the only stable equilibrium along the polygynous edge is the PP/P fixation point. Note

262 that maintaining both MP and PP queens in polygynous-only colonies requires very strong heterozygous

263 advantage, with MP queens more than twice as fit as PP queens (condition 6). This requirement for

264 strong selection emerges because, when mated with P males, only half of the daughters of MP queens

265 are MP, whereas all daughters of PP queens are PP.

266 We next considered the stability of these polygynous equilibria to the introduction of monogynous

267 genotypes (MM queens and M males), under random mating. We find that MM queens and M males

268 never spread when rare, from either the P-fixed or MP/PP equilibria. This is because almost all matings

269 involving a rare M male are with the common PP or MP females, which do not produce MM daughters

270 because of maternal-effect killing. Similarly, the vast majority of matings involving the rare MM queen

271 are with the common P male, which also do not generate MM daughters. Thus, the MM genotype rapidly

272   disappears from the population of queens, taking along with it the ability to produce M males. Even if

273   maternal-effect killing is strong but not complete, such that both $V^{\female}_{MM|MP \times M}$ and $V^{\male}_{M|MP}$ are small but not

274   zero, the monogynous genotypes do not invade under biologically reasonable conditions (with

275   exceptions only in the extreme case where the fitness of M males is so much higher than P males that

276   rare M males become common following a single bout of selection; see supplementary material). This

277   result, that monogynous colonies cannot establish when rare, holds whether or not colonies with MP

278   queens are able to recover the energy invested in lost embryos (i.e., whether or not $V^{\male}_{P|MP}$ is elevated due

279   to recovered resources following maternal-effect killing).

280   In short, if MP queens are much fitter than PP queens (condition 6 holds), then a genetic polymorphism

281   with both PP and MP queens can result, but the system consists of only polygynous colonies. In

282   particular, no matter how strong heterozygous advantage might be, a social polymorphism cannot be

283   maintained. Polygynous colonies can spread when rare if condition (4) holds, and the system converges

284   to one of the polygynous equilibria (with P fixed or with MP/PP queens), whereas monogynous colonies

285   cannot generally spread when rare. This result is in stark contrast to other systems, where a

286   polymorphism can be stably maintained by heterozygote advantage [27] or a balance between meiotic

287   drive and homozygous sterility/lethality [23].

288   We next illustrate the dynamics of the *F. selysi* system numerically. Because the frequency of males is

289   determined entirely by the genotype frequencies in their mothers (equation 3b), we initialize the male

290   frequencies according to equation (3b) using the current frequency of females, allowing us to closely

291   approximate the dynamics using only genotype frequencies among queens. We then visualize these

292   dynamics using ternary stream plots (Figures 2 and 3), where each corner of the triangle represents the

293   fixation of a queen genotype, the opposite edge corresponds to the absence of that genotype, and the

294   distance from the edge to the corner represents the frequency of that queen genotype. Arrows on the

295   stream plot represent the direction of the change in queen frequencies from different initial positions.

296   Figure 2 illustrates a case where the M-fixed equilibrium is stable along with either the P-fixed

297   equilibrium (panel a) or the MP/PP equilibrium (5) on the polygynous edge (panel b). In such cases, a

298   polymorphic internal equilibrium with all social types can exist but is unstable. Figure 3 illustrates a case

299   where the M fixed is unstable, in which case the only stable equilibrium is on the polygynous edge,

300   either the P-fixed equilibrium (panel a) or the MP/PP equilibrium (5) (panel b), and there is no

301   equilibrium with both monogynous and polygynous colonies.

302   Finally, we verified the above results numerically, confirming that a social polymorphism was never

303   stable using a numerical search. To conduct this search, we randomly drew one million sets of

304   parameters (all chosen uniformly between 0 and 1, other than the maternal-effect killing parameters

305   maintained at $V^{\female}_{MM|MP\times M} = V^{\male}_{M|MP} = 0$). For each parameter set, we numerically calculated all equilibria

306   and determined their stability properties, confirming that there was never a stable internal equilibrium

307   under random mating with both monogynous and polygynous colonies (see supplementary material for

308   all numerical results).
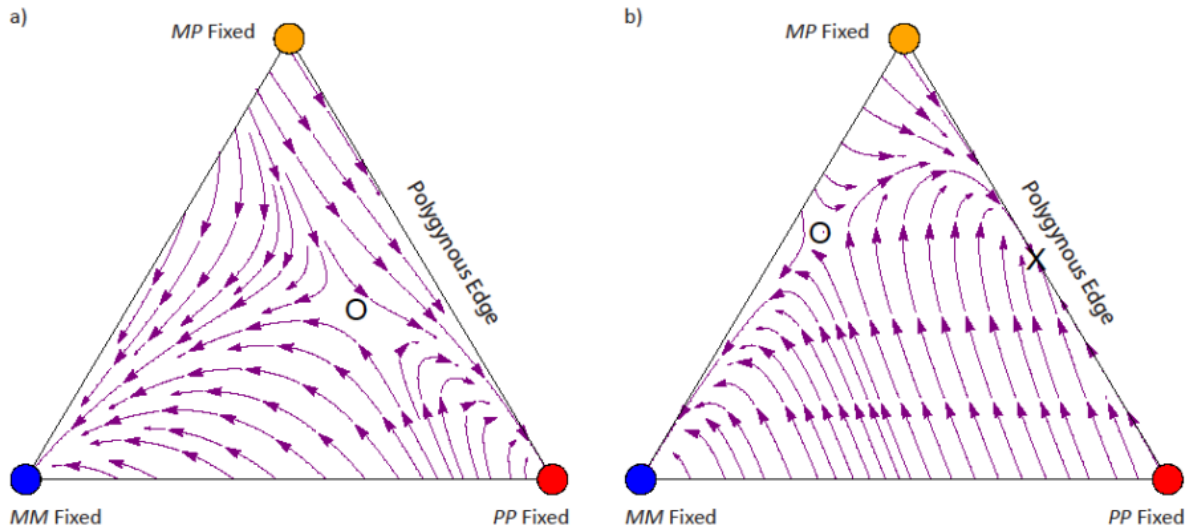
309   **Figure 2.** Stream plots show the dynamics of *F. selysi* queens when individuals in monogynous colonies
310   are most fit. The fixation of monogynous colonies (blue) is then stable to the spread of the *P* supergene
311   (condition 4 does not hold because *MM* queens and *M* males are sufficiently fit). (a) When heterozygous
312   females are low enough in fitness, the system evolves towards fixation of either *MM* females (blue) or
313   *PP* females (red) ($V^{\female}_{MP|ij\times k} = 1/5$). (b) When heterozygous females are intermediate in fitness, the
314   system can evolve towards fixation of either *MM* females (blue) or a polymorphism with both *MP* and
315   *PP* polygynous queens (marked by an ×) ($V^{\female}_{MP|ij\times k} = 3/5$). The open circle marks an unstable
316   equilibrium point. Other parameters: $V^{\female}_{MM|MP\times M} = V^{\male}_{M|MP} = 0$ (complete maternal-effect killing),
317   $V^{\female}_{MM|MM\times M} = 1$, and otherwise $V^{\male}_{a|ij} = V^{\female}_{ab|ij\times k} = 1/5$.
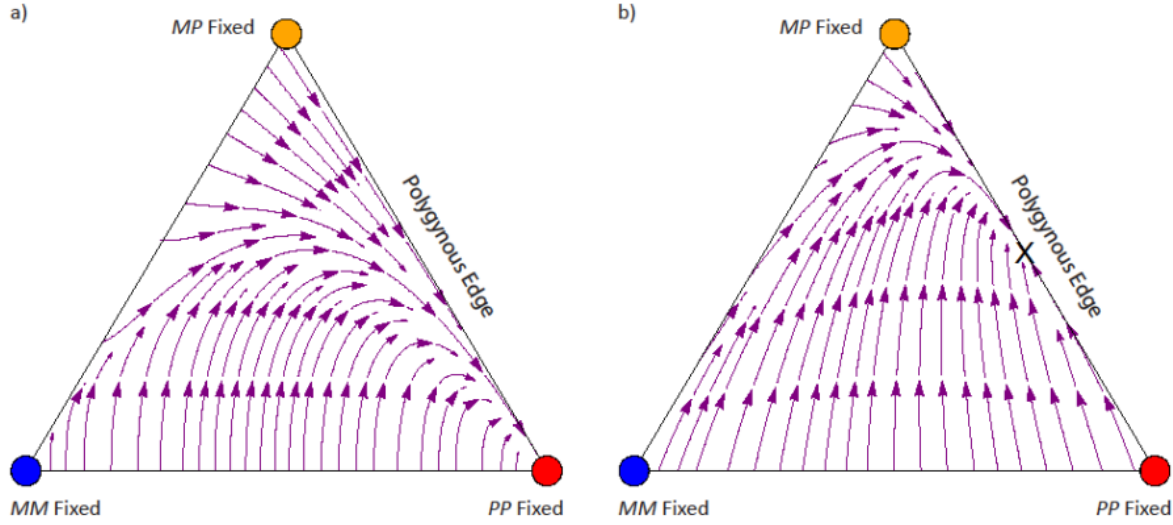
Figure 3. Stream plots show the dynamics of *F. selysi* queens when individuals in monogynous colonies are not more fit than individuals in polygynous colonies. The fixation of monogynous colonies (blue) is then unstable (condition 4 holds). (a) There are no fitness differences except those caused by maternal-effect killing, in which case *PP*-fixed is the only stable equilibrium (red). (b) There is heterozygous advantage, such that condition 6 holds, and *MP/PP* with only polygynous colonies is the only stable equilibrium (marked by an × on plot; $V_{MP|ij\times k}^{\female} = 3/5$). No internal equilibrium point exists in these cases. Other parameters: $V_{MM|MP\times M}^{\female} = V_{M|MP}^{\male} = 0$ (complete maternal-effect killing) and otherwise $V_{a|ij}^{\male} = V_{ab|ij\times k}^{\female} = 1/5$.

2) Variation in Fertility – Adding fertility differences alters equations (4) – (6) but does not qualitatively affect the outcome. In particular, there is never a case where both monogynous and polygynous haplotypes can spread when rare, except for biologically extreme male fitness differences. For example, with fertility differences ($R_{ij\times k} = f_{ij\times k} X_{ij} Y_k$), condition (4) determining when a monogynous social system is unstable to the introduction of polygyny becomes:

$$V_{MM|MM\times M}^{\female} f_{MM\times M} V_{M|MM}^{\male} < \frac{V_{MP|MM\times P}^{\female} f_{MM\times P} V_{P|MP}^{\male} + V_{MP|MP\times M}^{\female} f_{MP\times M} V_{M|MM}^{\male}}{2} \tag{7}$$

Similarly, condition (6) determining when polygynous-only colonies will evolve towards an equilibrium with both *MP/PP* becomes:

$$V_{PP|PP\times P}^{\female} f_{PP\times P} < \frac{V_{MP|MP\times P}^{\female} f_{MP\times P}}{2} \tag{8}$$

15

335   Again, however, monogynous colonies can never spread when rare within a system consisting only of

336   polygynous colonies. Furthermore, a numerical search across one million randomly drawn parameter

337   sets failed to find any case of a stable social polymorphism.

338   Therefore, we have shown that, under a broad range of conditions including arbitrary fertility

339   differences, there is not a protected polymorphism where both monogynous and polygynous forms can

340   spread when rare. Consequently, we would not expect a social polymorphism to be maintained under

341   random mating, with or without fertility differences, because of the strong constraints imposed by

342   maternal-effect killing. Graphically, the problem is that the polygynous edge, consisting of only PP and

343   MP queens in Figures 2 and 3, is always strongly absorbing because neither rare M males nor rare MM

344   queens produce MM daughters: rare M males mate predominantly with common MP/PP queens whose

345   daughters are never MM because of maternal-effect killing, and MM queens mate predominantly with

346   common P males whose daughters are never MM by the rules of inheritance.

347   *3) Sexual Selection* – The same conclusions regarding invasion of rare M and P haplotypes hold true

348   with sexual selection using the fixed relative preference scheme of Kirkpatrick [24], where $R_{ij \times k} =$

349    $X_{ij} \frac{\alpha_{ij \times k} Y_k}{\alpha_{ij \times P} Y_P + \alpha_{ij \times M} Y_M}$. In this case, invasion analysis gives the same result as (7), setting $f_{MM \times M} =$

350    $f_{MP \times M} = 1$ and $f_{MM \times P} = \frac{\alpha_{MM \times P}}{\alpha_{MM \times M}}$ (because P males are rare and the Y_P term in the denominator of $R_{ij \times k}$

351   is negligible to leading order in the analysis). Similarly, equation (8) determining which equilibrium is

352   stable along the polygynous edge continues to hold, where now $f_{PP \times P} = f_{MP \times P} = 1$ given that only P

353   males are present along this edge. Most importantly, polygynous-only colonies are always stable to the

354   introduction of MM queens and M males, regardless of the values of $\alpha_{ij \times k}$, when the mating scheme is

355   proportional to the product of the frequency of both mates.

356   In the cases discussed thus far (random mating, fertility differences, and sexual selection with fixed

357   relative preferences), monogynous colonies can never invade when very rare. However, with very strong

358   sexual preferences, MM queens can so strongly prefer M males that monogynous colonies can be

359   maintained, once they rise to a sufficiently high frequency. In this case, a stable social polymorphism

360   may exist under extreme preference differences (see supplementary material for specific description of

361   parameter conditions required). Figure 4 illustrates one example, where MM queens prefer to mate with

362   M males almost 100 times more than P males, allowing M to spread from intermediate frequency even

363   though it cannot spread when rare. Importantly, a numerical search indicates that the degree of

16

364   preference of queens for males of their own social form must differ between monogynous and

365   polygynous queens in order to stabilize a social polymorphism. When monogynous and polygynous

366   queens had the same degree of preference for males belonging to their own social form, a numerical

367   search of one million random parameter sets found no stable social polymorphism. Note that with sexual

368   selection and fixed relative mating preferences [24], if *MM* queens have a strong preference for *M*

369   males, then mating becomes effectively assortative, because *MM* females search until finding an *M*

370   mate.
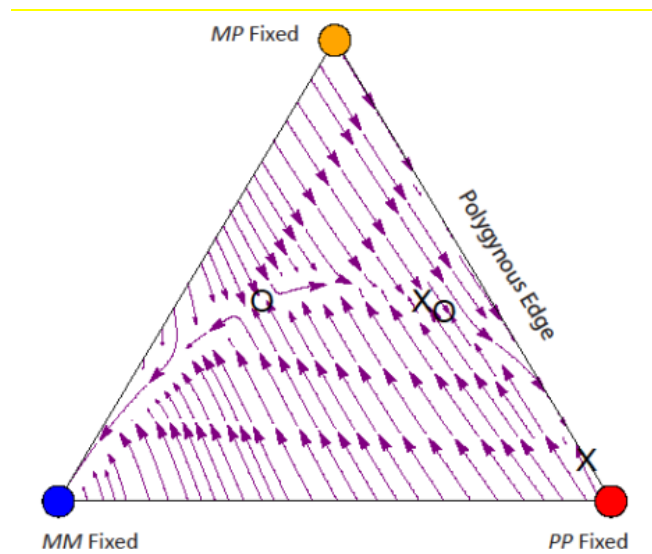
371 **Figure 4.** Stream plot showing the dynamics of *F. selysi* queens with sexual selection such that queens
372 exhibit fixed relative mating preferences [24]. Here we illustrate a case when populations composed of
373 only monogynous colonies or only polygynous colonies are both stable (condition 4 holds). The open
374 circles mark unstable equilibrium points and the ×'s mark stable equilibrium points. Parameters:
375 $\frac{f_{MM \times M}}{f_{MM \times P}} = 96$ (an extremely strong preference), $\frac{f_{MP \times P}}{f_{MP \times M}} = \frac{f_{PP \times P}}{f_{PP \times M}} = 1.47$, $V^{\female}_{MM|ij \times k} = 0.46$, $V^{\female}_{MP|ij \times k} =$
376 $0.69, V^{\female}_{PP|ij \times k} = 0.33, V^{\female}_{MM|MP \times M} = V^{\male}_{M|MP} = 0$ (complete maternal-effect killing), and $V^{\male}_{a|ij} = 1$ (males
377 have the same viability).

378   *4) Assortative Mating* – Given the above results, we conjectured that a key feature necessary for both

379   social haplotypes to spread when rare and maintain a social polymorphism is assortative mating, such

380   that rare individuals can find and mate with similarly rare partners belonging to the same social form. A

381   variety of mating schemes can produce assortative mating, for example when queens actively seek their

382   preferred mate or when mating occurs near or within colonies.

383   We thus introduce assortative mating by social form, allowing mating among members of the same

384   colony type. Specifically, we assume monogynous queens mate exclusively with *M* males at some

17

385 frequency, m_M, and otherwise mate randomly, while polygynous queens mate with P males at some

386 frequency, m_P, and otherwise mate randomly. We allow the two social morphs to mate assortatively at

387 different rates because of empirical results indicating that monogynous queens have more often mated

388 assortatively than polygynous queens [19]. With assortative mating by social form, we have:

389 $$R_{MM \times M} = (1 - m_M) X_{MM} Y_M + m_M X_{MM} \qquad (9)$$

390 $$R_{MM \times P} = (1 - m_M) X_{MM} Y_P$$

391 $$R_{MP \times M} = (1 - m_P) X_{MP} Y_M$$

392 $$R_{MP \times P} = (1 - m_P) X_{MP} Y_P + m_P X_{MP}$$

393 $$R_{PP \times M} = (1 - m_P) X_{PP} Y_M$$

394 $$R_{PP \times P} = (1 - m_P) X_{PP} Y_P + m_P X_{PP}$$

395 In the absence of MM female or M males, we again have two possible equilibria on the polygynous

396 edge, with only P males present and either PP queens or a PP/MP polymorphism, given by equation (5)

397 (details of the stability analyses are given in the supplementary material). On this edge, the MP/PP

398 equilibrium is stable if (6) holds, and otherwise the P-fixed equilibrium is stable.

399 With assortative mating, it is now possible, however, for the equilibria on the polygynous edge to be

400 unstable to the introduction of MM queens and M males. Specifically, when haplotype P is fixed,

401 monogynous colonies spread when rare if:

402 $$V^{\female}_{PP|PP \times P} < m_M V^{\female}_{MM|MM \times M} \qquad (12a)$$

403

404 Alternatively, if polygynous colonies consist of PP and MP queens at equilibrium (equation 5), then

405 monogynous colonies spread when rare if:

406 $$\frac{V^{\female}_{MP|MP \times P}}{2} < m_M V^{\female}_{MM|MM \times M} \qquad (12b)$$

407 Notice that the relative magnitudes of the left-hand sides of (12) determine which equilibrium is stable

408 along the polygynous edge (equation 6). Whichever value is larger determines the composition of

409 polygynous colonies against which rare monogynous colonies must compete. In either case, the key

410 feature is that rare MM queens are able to find and mate with rare M males, regardless of how rare they

18

411   are. Only this feature allows monogynous colonies to escape the strongly absorbing polygynous edge

412   caused by maternal effect killing and to establish when rare.

413   In addition, under certain conditions, polygynous colonies can also spread within a fully monogynous

414   population. Analyzing the invasion of P into a population fixed on M involves solving a cubic equation

415   for the leading eigenvalue (see supplementary material). When there is complete assortment ($m_M =$

416   $m_P = 1$), this cubic equation factors, allowing us to determine that P will spread if either of these

417   conditions is met:

418
$$V^{\female}_{PP|PP \times P} > V^{\female}_{MM|MM \times M} \tag{13a}$$

419
$$\frac{V^{\female}_{MP|MP \times P}}{2} > V^{\female}_{MM|MM \times M} \tag{13b}$$

420   These conditions for the spread of P when rare with complete assortative mating contradict the

421   conditions for the spread of M when rare. Effectively, with complete assortative mating, the system

422   quickly approaches two isolated sub-populations consisting of {MM,M} and either {PP,P} or

423   {PP,MP,P} individuals (whichever polygynous set is more fit). Without genetic exchange between these

424   sub-populations, either the monogynous sub-population {MM,M} is more fit and fixes or is less fit and

425   disappears. Either way, a social polymorphism is not possible with complete assortative mating by social

426   form. This was confirmed in a numerical search across one million randomly chosen parameter sets.


427   Thus, with either random mating ($m_M = m_P = 0$) or with complete assortative mating by social form

428   ($m_M = m_P = 1$), a stable social polymorphism does not exist. With an intermediate rate of assortative

429   mating by social form, however, a social polymorphism can result (Figure 5). For example, if the P-

430   fixed equilibrium is stable along the polygynous edge, it is now possible for M to spread when rare if

431   assortative mating is sufficiently high in monogynous colonies, as long as MM queens are fitter than PP

432   queens, and for P to spread when rare if MP queens are fitter than MM queens. Both social haplotypes

433   can invade when rare even if selection is weak (all $V^{\male}_{a|ij}$ and $V^{\female}_{ab|ij \times k}$ near 1, except for $V^{\female}_{MM|MP \times M} =$

434   $V^{\male}_{M|MP} = 0$ due to maternal-effect killing), as long as:

435
$$(1 - m_P)^2 < (1 - m_M) < V^{\female}_{MM|MM \times M} - V^{\female}_{PP|PP \times P} \tag{14}$$

19

436 This result requires that $V^{\female}_{MM|MM \times M} > V^{\female}_{PP|PP \times P}$ and that monogynous queens mate assortatively at a

437 very high rate (but not exclusively). Note that the more that polygynous queens mate assortatively (the

438 higher m_P, including $m_P=1$), the easier this condition is to satisfy.

439 *Complete assortative mating in monogynous queens*

440 As queens heading mature monogynous colonies have exclusively mated with M males, while

441 polygynous queens have mostly, but not exclusively, mated with P males [19], we first focus

442 numerically on cases where $m_M = 1$ and explore the conditions needed for the maintenance of a

443 polymorphism. With complete assortative mating ($m_M = 1$) and when males are assumed equally fit, a

444 stable social polymorphism is possible, but only when there is strong heterozygous advantage, as

445 illustrated in Figure 5. For some parameters, there are two separate stable equilibria (grey dots in Figure

446 5a), one is a stable social polymorphism and the other is fixed for the M haplotype. These cases tend to

447 be found when polygynous queens often mate randomly (low m_P). Such systems are, however, prone to

448 losing social polymorphism. For example, the colonization of new environments by monogynous queens

449 could result in the loss of polygynous colonies, and such populations would then resist invasion by rare

450 P haplotypes. When polygynous queens mate assortatively at a higher rate (intermediate m_P), the P

451 haplotype is more likely to spread when rare, leading to cases where the only stable polymorphism

452 involves a social polymorphism (red dots in Figure 5a), which better resist loss of the polygynous type.
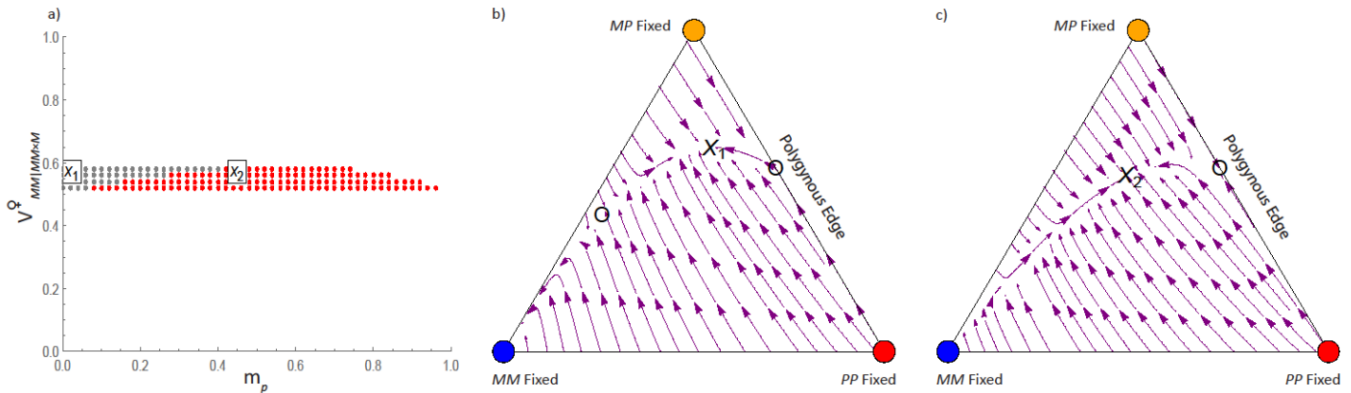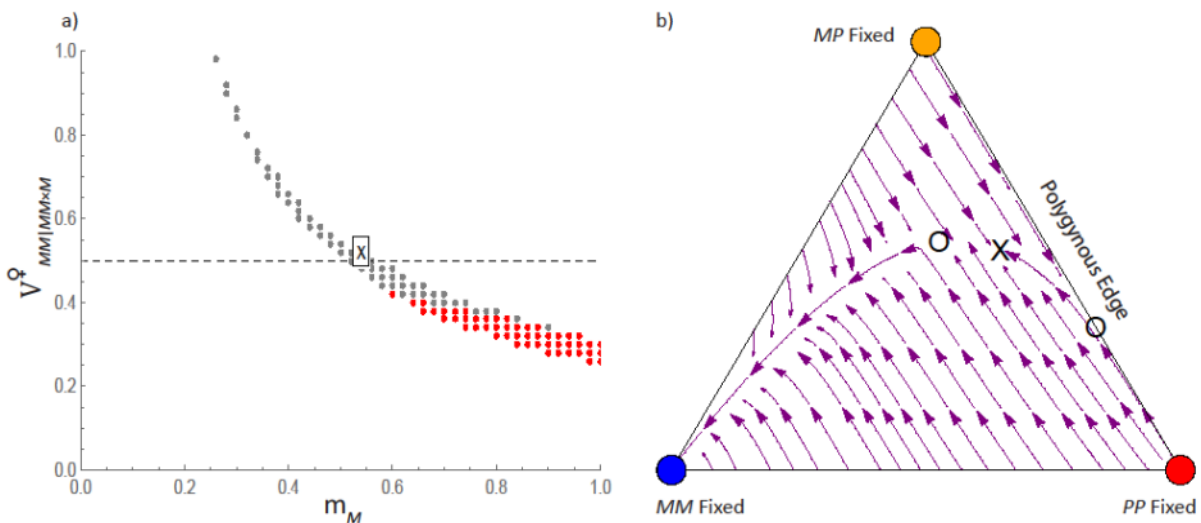

453 **Figure 5.** The maintenance of social polymorphism is possible with assortative mating by social form,
454 here illustrated with complete assortative mating in monogynous queens and partial assortative mating in
455 polygynous queens. Here, *MM* queens only mate with M males ($m_M = 1$). Panel (a) shows the range of
456 assortative mating in polygynous colonies (m_P) and the viability of monogynous queens ($V^{\female}_{MM|MM \times M}$)
457 for which a stable social polymorphism persists when $V^{\female}_{MP|ij \times k} = 1$ and $V^{\female}_{PP|PP \times P} = 0.3$. Grey dots: both
458 a social polymorphism and M-fixed equilibria are stable. Red dots: only the social polymorphism is

459 stable. Panels (b) and (c) show stream plots for the parameter sets indicated in panel a (panel b at x_1,
460 panel c at x_2). Open circles mark unstable equilibrium points, while $\times_1$ and $\times_2$ indicate stable internal
461 equilibrium points. Other parameters: $V^{\female}_{MM|MP\times M} = V^{\male}_{M|MP} = 0$ (maternal-effect killing) and otherwise
462 $V^{\male}_{a|ij} = V^{\female}_{ab|ij\times k} = 1$.

Incomplete assortative mating in monogynous queens

464 Recent field work has shown that monogynous queens sampled from mating swarms do mate with P
465 males [20], with $m_M = {\sim}\,0.65$, even though this cross is not observed in mature monogynous colonies
466 [15, 19]. We thus relax the assumption that $m_M = 1$ and explore the conditions under which a
467 polymorphism can be maintained. In the numerical cases explored, as the rate of assortative mating by
468 monogynous queens declines, the M haplotype must be increasingly fit for a social polymoprhism to be
469 stably maintained (recall that it is assortative mating that protects the M haplotype from being eliminated
470 by maternal effect killing in MP daughters produced when MM queens mate with P males). For
471 example, with the parameters in Figure 6a, there must be heterozygote advantage with MM queens less
472 fit than MP queens under intermediate to high rates of assortment (m_M above 0.6), but there must be
473 directional selection favoring MM queens under low to intermediate rates of assortment (m_M between
474 0.2 and 0.6), with no stable polymorphism possible for weaker assortment. Again, for each set of
475 parameters that ensures a stable social polymorphism, the fixation of the M haplotype may (grey points
476 in Figure 6a, stream plot in Figure 6b) or may not (red points in Figure 6a) be a separate stable
477 equilibrium (see supplementary material).

478 **Figure 6.** Partial assortative mating by both social forms allows for the maintenance of social
479 polymorphism. Panel (a) shows the range of assortative mating by social form in monogynous colonies

480   (m_M) and the viability of monogynous queens $(V^{\female}_{MM|MM\times M})$ for which a social polymorphism persists.
481   Above the dashed line corresponds to directional selection favouring the M haplotype in females, while
482   below the dashed line there is heterozygous advantage. Grey dots: both a social polymorphism and M-
483   fixed equilibria are stable. Red dots: only the social polymorphism is stable. Panel (b) shows the stream
484   plot for a parameter set (marked by an $\times$ in panel a) that permits a stable internal equilibrium denoted by
485   an $\times$ in panel b ($m_M = 0.54, V^{\female}_{MM|MM\times M} = 0.52$). Open circles mark unstable equilibrium points. Other
486   parameters are as in Figure 5 except $V^{\female}_{MP|ij\times k} = 0.5, V^{\female}_{PP|ij\times k} = 0.2$, and $m_P = 0.5$.

487   In summary we find that, under the right balance of parameters (as illustrated in Figures 5 and 6),

488   assortative mating of monogynous queens allows for the spread of monogynous colonies when rare. For

489   example, if selection is weak (all $V^{\male}_{a|ij}$ and $V^{\female}_{ab|ij\times k}$ near 1, except for $V^{\female}_{MM|MP\times M} = V^{\male}_{M|MP} = 0$ due to

490   maternal-effect killing), for a social polymorphism to be maintained, this balance requires that both

491   monogynous and polygynous queens mostly, but not always, mate assortatively, in such a way that

492   equation 14 is satisfied. Although constitutive costs of assortative mating are incorporated in the

493   viability terms, we have not incorporated frequency-dependent costs of assortative mating. If costs rise

494   with the rarity of similar mates, we expect that it would be harder to maintain a social polymorphism

495   because rare genotypes would pay that cost and be less likely to spread (particularly, rare monogynous

496   types would be less able to spread near the polygynous edge).

497   The results above do not change substantially when assortative mating depends on genotype, rather than

498   on social type, with MP queens mating equally with M and P males (except that the equivalent to

499   condition (5) for a social polymorphism under weak selection is never satisfied; see supplementary

500   material). While assortative mating, by either social form or genotype, does allow the maintenance of a

501   social polymorphism (Figures 5 and 6), the conditions for stability are restrictive, requiring a delicate

502   balance of selection among genotypes depending on the strength of assortment (e.g., Figure 6a).

503   **Discussion**

504   Selfish genetic elements favouring their own transmission are ubiquitous across the tree of life, yet

505   explaining their dynamics and observed frequencies in natural systems is challenging [6, 28]. In short,

506   when a genetic element drives, what prevents it from reaching fixation and becoming undetectable due

507   to the lack of polymorphism? Maternal-effect post-segregational killers have been detected in ants [8],

508   beetles [29], nematodes [30] and many bacteria, including endosymbionts [6, 9]. In such systems, a

509   maternally-expressed toxin linked to a zygotically-expressed antidote causes the death of progeny that

510   did not inherit the element [9, 31]. Simple population genetic models show that these selfish genetic

511   elements are expected to increase in frequency and that high fitness costs of the elements are needed to

512   prevent their fixation [28, 32]. Supergenes controlling complex phenotypes are prone to harbour selfish

513   genetic elements, yet the effect of drive on their evolutionary dynamics had not been modeled so far.

514   We have modeled the dynamics of a supergene controlling colony social organization in the Alpine

515   silver ant, *F. selysi*, exploring a broad range of fitness functions and mating regimes and incorporating

516   the transmission ratio distortion caused by maternal-effect killing by the *P* haplotype [8]. A key finding

517   of the model is that maternal-effect killing creates such an imbalance in the selective forces acting that it

518   is challenging to account for the long-term persistence of both social forms, i.e. monogynous colonies

519   with a single queen and polygynous colonies with multiple queens. Indeed, there is no stable

520   polymorphic equilibrium in any model with constant fitnesses and mating regimes that did not generate

521   assortative mating. Essentially, maternal-effect killing prevents rare monogynous colonies from

522   invading populations of polygynous colonies whenever rare *MM* queens mate predominantly with the

523   common type of male (*P*), producing *MP* daughters that do not regenerate *MM* queens or *M* males.

524   For both social forms to be protected from loss when rare (i.e., for there to be no stable equilibrium with

525   only one social form), we find that there must be strong assortative mating, so that *MM* queens

526   frequently mate with *M* males even when both are rare, with the right balance of fitnesses involving

527   strong selective differences among genotypes (e.g., Figures 5 and 6) or very high, but not complete,

528   assortative mating by both social types (equation 14). Alternatively, there may be a stable social

529   polymorphism alongside stable equilibria with only one social haplotype, which we observed with

530   assortative mating (including with sexual selection when fixed-relative preferences were so strong that

531   assortment arose). The latter cases are, however, more prone to losing social polymorphism, if by chance

532   one social form goes locally extinct. Whether the restrictive conditions allowing a social polymorphism

533   are satisfied in Alpine silver ants remains an open question, as discussed below.

534   In many supergenes, one haplotype is a homozgyous lethal, which selects for disassortative mating [33].

535   The Alpine silver ant system is unusual, as both homozygotes are viable. Moreover, maternal effect

536   killing by the *P* haplotype may select for assortative mating by *MM* queens for *M* males and *MP* queens

537   for *P* males, respectively. In line with that prediction, effective mating in Alpine silver ants appears to be

538   strongly assortative: when analysing queens heading mature field colonies, all *MM* queens had mated

539   with *M* males, while *MP* and *PP* queens had mated mostly with *P* males [77%; 15, 19]. The proximate

540   mechanisms underlying this pattern of assortative mating remain unclear. In mate choice experiments in

23

541   captivity, queens and males mated randomly with respect to social form [21], but the experimental

542   conditions may have interfered with natural mate choice. In the field, queens and males from each social

543   form fly away from their natal colony to join mating swarms, where *MM* queens mate mostly

544   assortatively ($m_M \sim 0.65,$ based on mating swarm data in [20]). Queens in monogynous colonies do

545   not mate with members of the same colony [19]. Hence, the assortative mating pattern observed in the

546   field is consistent with a major condition for stability in the model, but we do not know whether and

547   how *MM* queens actually seek out and mate preferentially with *M* males when both are rare, as required

548   to maintain the social polymorphism. Assortative mating appears easier to achieve within the

549   polygynous social form, as *PP* or *MP* queens as well as *P* males may mate within or close to their natal

550   colony.

551   Regarding the strength and direction of selection, it is extremely difficult to obtain precise estimates of

552   fitness, given that silver ant queens are long-lived and iteroparous [13]. Moreover, the two social forms

553   differ in morphology, sex allocation, colony size and other life-history traits, which hampers fitness

554   comparisons [13, 34, 35]. Queens from alternative social forms may well differ in fitness, as they

555   typically use alternative modes of dispersal and colony founding [independent colony founding versus

556   budding; 25]. Queens from monogynous colonies disperse on the wing and found colonies

557   independently, while queens from polygynous colonies have the additional options of staying in their

558   natal colony, seeking adoption in other colonies, founding colonies with the help of workers or in

559   assocation with other queens [36]. Queens from monogynous colonies are more fertile and more

560   successful at independent colony founding in harsh ecological conditions than queens of polygynous

561   origin [21, 26, 37]. The accumulation of deleterious mutations in the non-recombining supergene can

562   also cause fitness differences among genotypes. In particular, deleterious mutations that primarily affect

563   females can accumulate in the *P* haplotype yet be masked in *MP* polygynous queens (by contrast,

564   mutations in monogynous colonies are never masked in *MM* queens). Recent studies in the field and

565   laboratory revealed that *PP* females have lower survival, fertility, and fecundity than *MP* females

566   (Blacher, De Gasperin, Grasso, Sarton-Lohéac, Alleman and Chapuisat, unpublished results). Overall,

567   life-history and dispersal differences between social forms, combined with a recessive genetic load that

568   can accumulate in the *P* haplotype, might thus create fitness differences between supergene genotypes

569   that contribute to stabilizing the polymorphism (e.g., as seen in Figure 5).

570   While general in many respects, our model does not investigate all forms of frequency- or density-

571   dependent selection. Frequency-dependent selection may arise from antagonistic interactions [38]. For

24

example, if one social form is more aggressive than the other, it may be favoured when rare, and disfavoured when common. Spatially-varying selection due to habitat heterogeneity may also stabilize the polymorphism [17, 39]. In particular, monogynous queens may be better at dispersing and colonizing novel or patchy habitats, while polygynous queens may outperform monogynous ones in old, continuous and saturated habitats, due to their larger colony size and possibility of establishing novel colonies by budding [13, 17, 25]. Such ecological niche differentiation could maintain both types, just as it can maintain different species, but it would not explain why mating between social forms persists, as the continued gene flow between the types prevents further genetic adaptation of each social form to its specialized ecological niche.

Supergenes, such as found in Alpine silver ants, typically affect multiple morphological, physiological and behavioral traits [1], and over time they tend to accumulate recessive deleterious mutations [5] and selfish genetic elements [8]. The *P* haplotype of *F. selysi*, which is derived and differs by several inversion from the ancestral *M* haplotype, causes selfish post-segregational killing [8, 16]. The supergene that controls social organization in the fire ant *Solenopsis invicta* also causes unusual patterns of segregation distortion and genotype-specific mortality [7, 40, 41]. In mice, the *t*-haplotype not only distorts segregation, it also affects sperm competition and increases dispersal propensity [23, 42, 43]. The *Segregation Distorter* supergene in fruit flies has diverse effects on fitness and sex ratio [44]. In many empirical cases, the driven or positively selected supergene haplotype is a homozygous lethal but has lower frequencies than expected by simple models [45]. Although the details of each system differ, our model shows that explaining the long-term maintenance of selfish supergenes is not trivial. Overall, the drive induced by maternal-effect killing in Alpine silver ants destabilizes the polymorphism and prevents rare monogynous colonies from invading populations fixed for polygynous colonies. Under the broad range of models considered here, a stable polymorphic equilibrium can only be reached under a regime of strong but not complete assortative mating, combined with the right balance of fitnesses for alternative supergene genotypes.

Acknowledgements

603 **Supplementary material**

604 • *Mathematica* file with all main analyses

605 • Numerical searches and local stability analyses

606 **Authors' Contributions**

607 A.G., S.O. and M.C. conceived the study. A.G. and S.O. developed the model. A.G. performed the

608 numerical analysis, analysed the results and drew the figures. A.G., S.O. and M.C. interpreted the results

609 and wrote the manuscript. All authors approved the final version.

610 **References**

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Appendix: Table of parameters

Symbol	Meaning
i,j,k	Individual social alleles carried by the parents
a,b	Individual social alleles carried by the offspring
X_{ij}	Frequency of queens with ij genotype (X'_{ij} in next generation)
Y_k	Frequency of males with k genotype (Y'_k in next generation)
$O^{\female}_{ab|ij \times k}$	Production rate of surviving ab queen offspring from ij queen and k male parents
$O^{\male}_{a|ij}$	Production rate of surviving a male offspring from ij queens
$R_{ij \times k}$	Frequency of crosses between queens of genotype ij and males of genotype k
$V^{\female}_{ab|ij \times k}$	Viability of ab queen offspring from ij queen and k male parents
$V^{\male}_{a|ij}$	Viability of male offspring with genotype a produced by ij queens
$f_{ij \times k}$	Offspring fertility of an ij queen and k male parents
$\alpha_{ij \times k}$	Fixed relative-preference of an ij queen for k males
m_i	Frequency of assortative mating where queens with social type i mate exclusively with i males
$\sum\limits_{ij,k}$	Sum over all possible mating pairs
$\sum\limits_{ab,ij,k}$	Sum over all possible mating pairs and queen offspring
$\sum\limits_{ij}$	Sum over all queens
$\sum\limits_{a,ij}$	Sum over all queens and male offspring