doi:10.1111/evo.14585

SSE SOCIETY for the STUDY of EVOLUTION

Paternal genome elimination promotes altruism in viscous populations

Thomas J. Hitchcock[1,2] **and Andy Gardner**[1]

[1]*School of Biology, University of St Andrews, St Andrews KY16 9TH, United Kingdom*

[2]*E-mail: th76@st-andrews.ac.uk*

Received December 15, 2021
Accepted July 4, 2022

Population viscosity has long been thought to promote the evolution of altruism. However, in the simplest scenarios, the potential for altruism is invariant with respect to dispersal—a surprising result that holds for haploidy, diploidy, and haplodiploidy (arrhenotoky). Here, we develop a kin-selection model to investigate how population viscosity affects the potential for altruism in species with male paternal genome elimination (PGE), exploring altruism enacted by both females and males, and both juveniles and adults. We find that (1) PGE promotes altruistic behaviors relative to the other inheritance systems, and to a degree that depends on the extent of paternal genome expression. (2) Under PGE, dispersal increases the potential for altruism in juveniles and decreases it in adults. (3) The genetics of PGE can lead to striking differences in sex-specific potentials for altruism, even in the absence of any sex differences in ecology.

KEY WORDS: **Dispersal, haplodiploidy, inbreeding, intragenomic conflict, paternal genome elimination, social behavior.**

> "over a range of different species we would expect to find giving traits commonest and most highly developed in the species with the most viscous populations."
>
> – Hamilton (1964a)

> "the point is that, to be effective, altruism must put offspring into competition with non-altruists, not bunch them in a wasteful competition with their own kind."
>
> – Hamilton (1971)

Population viscosity has long been suggested to promote the evolution of altruistic behavior, because when individuals remain close to their place of birth during the course of their lives, they will often be closely related to their neighbors, such that even indiscriminate altruism will tend to primarily benefit their genetic relatives (Hamilton 1964a,b). However, alongside increased relatedness, population viscosity also increases the extent to which individuals compete with those same relatives for resources, that is, kin competition (Hamilton 1971, 1975; Alexander 1974; Frank 1998). Under the simplest of models—including the infinite, inelastic island model of population structure—these two effects of increased relatedness and increased kin competition exactly cancel, such that the rate of dispersal has no net impact on the level of altruism that is evolutionarily favored (Taylor 1992a,b; Wilson et al. 1992; Queller 1994; West et al. 2002). This finding has sparked a body of theoretical research into understanding when and why this cancellation effect may break down, examples of which include overlapping generations (Taylor and Irwin 2000; Irwin and Taylor 2001), budding dispersal (Gardner and West 2006), sex-biased dispersal (Johnstone and Cant 2008; Gardner 2010), and density-dependent dispersal (Kanwal and Gardner 2022), among others (see Cooper et al. 2018 for an overview).

The primary focus of this theoretical work has been on ecological factors, and relatively little work has been done to investigate whether alternative genetic systems may cause this cancellation result to break down. One reason might be that Taylor's (1992a) analysis, which launched this avenue of inquiry, already obtained results for haploidy, diploidy, and haplodiploidy (more specifically arrhenotoky), and found that the cancellation holds under all three genetic systems (Taylor 1992a). Although this might suggest that the cancellation result holds robustly in the face of variation in genetic system, more recent results hint that this need not be the case. Specifically, Yeh and Gardner's (2012) general-ploidy version of Taylor's (1992a) original

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model reveals that the cancellation breaks down in unusual scenarios whereby one sex contributes genes to the other sex but not vice versa. Similarly, a recent model of the evolution of male harm investigated cases of imperfectly uniparental transmission of cytoplasmic genes, finding that this, too, results in social behavior that is not invariant with respect to the rate of dispersal (Hitchcock and Gardner 2021). However, the extent to which different inheritance systems may decouple viscosity's effects upon relatedness and kin competition remains obscure.

An understudied genetic system that may be of particular interest is that of male paternal genome elimination (PGE; Haig 2002; Burt and Trivers 2006; Gardner and Ross 2014; de la Filia et al. 2015; Hodson et al. 2017; Jaron et al. 2022). Under this system—which is found in groups of flies, springtails, mites, coccids, and beetles—males receive, but do not transmit, a paternal genome. This paternal genome, although not transmitted, may nonetheless influence the phenotype of the male, with the extent of this influence determined by the developmental timing of the paternal genome's elimination and the extent of the paternal genome's expression, factors that vary between tissues and species (de la Filia et al. 2015, 2018). Thus, although the transmission genetics of PGE are equivalent to "conventional" haplodiploidy (i.e., arrhenotoky), the somatic genetics differs, with both males and females being diploid. Recent years have seen increased interest in PGE systems, not only because they include economically important pests (e.g., the coffee borer beetle), but also because, with the advent of new genomic tools, their remarkable genetics enables potentially exceptional tests of evolutionary theory (Featherston et al. 2013; de la Filia et al. 2015; Klein et al. 2021; Hitchcock et al. 2022).

Here, we construct a kin selection model to investigate how population viscosity alters the potential for altruism in haploid, diploid, haplodiploid (arrhenotokous), and male PGE species. We consider altruism enacted by both males and females, and at both juvenile (predispersal) and adult (postdispersal) stages, allowing for various sex biases in demography. We find that (1) PGE promotes altruistic behaviors relative to the other inheritance systems, with the extent of this shaped by the degree of paternal genome expression; (2) unlike diploidy and arrhenotoky, dispersal does alter the potential for altruism in PGE species, with the direction of this effect dependent on the point in the life cycle that the altruism is expressed; and (3) PGE's asymmetric genetics can lead to striking differences in sex-specific potentials for altruism, even without any further sex-specific ecology being assumed.

Methodology

We consider an infinite population subdivided into patches, whereby on each patch there reside a large number of juveniles born to n females and n males. These juveniles invest in a social behavior that modulates their survival to adulthood S, with a focal individual's survival being determined both by their own investment x_j and also by the investment of their social partners y_j: specifically, we have $\partial(S/\bar{S})/(\partial x_j) = -c_j$ for self and $\partial(S/\bar{S})/(\partial y_j) = b_j$ for social partners, where $\bar{S}$ is the mean survival of juveniles in the population. Individuals then disperse from their patch with probability d. Following dispersal, individuals compete for representation within the n breeding adults of each sex on each patch, with all unsuccessful individuals dying. Adults then engage in further social interactions that modulate their fecundity F, with a focal individual's fecundity modulated both by their investment x_a, the investment of their same-sex social partners y_a, and of their opposite-sex social partners y'_a: specficially, we have $\partial(F/\bar{F})/\partial x_a = -c_a$, $\partial(F/\bar{F})/\partial y_a = b_a$, and $\partial(F/\bar{F})/\partial y'_a = b_a - c_a$, where $\bar{F}$ is the mean fecundity of adults in the population. After new offspring are born, the adults on the patch then die and the life cycle begins once more. This life cycle thus encompasses the model of Gardner (2010), which investigated the social behavior of juveniles, and the model of Johnstone and Cant (2008), which investigated the social behavior of adults, although without any sex differences in ecology. Further details on this life cycle and its associatced fitness functions, plus extensions to sexual asymmetries in both dispersal and the number of breeders, are given in Supporting Information S1–S3.

We determine the conditions under which natural selection favors an increase in the level of these two social traits using the kin-selection methodology of Taylor and Frank (Taylor 1996; Taylor and Frank 1996; Frank 1998; Taylor et al. 2007). This approach analyzes how the relative fitness of a focal individual is altered by both small changes in their own trait value and by correlated changes in the trait values of their social partners, with the extent of phenotypic correlation being determined by their relatedness to those social partners (Supporting Information S4). These changes in relative fitness are then weighted by the reproductive value of the focal individual's class (Supporting Information S5). These methods assume that selection is weak and that there is vanishingly little genetic variation, in order that the powerful tools of differential calculus be brought to bear on the problem. For this analysis, we treat juvenile and adult social behaviors as independently evolving traits that may show sex-limited expression.

As we investigate altruistic behavior, we restrict our attention to scenarios in which juvenile social behavior incurs a positive survival cost for self (i.e., $c_j > 0$) and provides a positive survival benefit for social partners (i.e., $b_j > 0$), and in which adult social behaviour incurs a positive fecundity cost to oneself and to ones mating partners (i.e., $c_j > 0$) and provides a

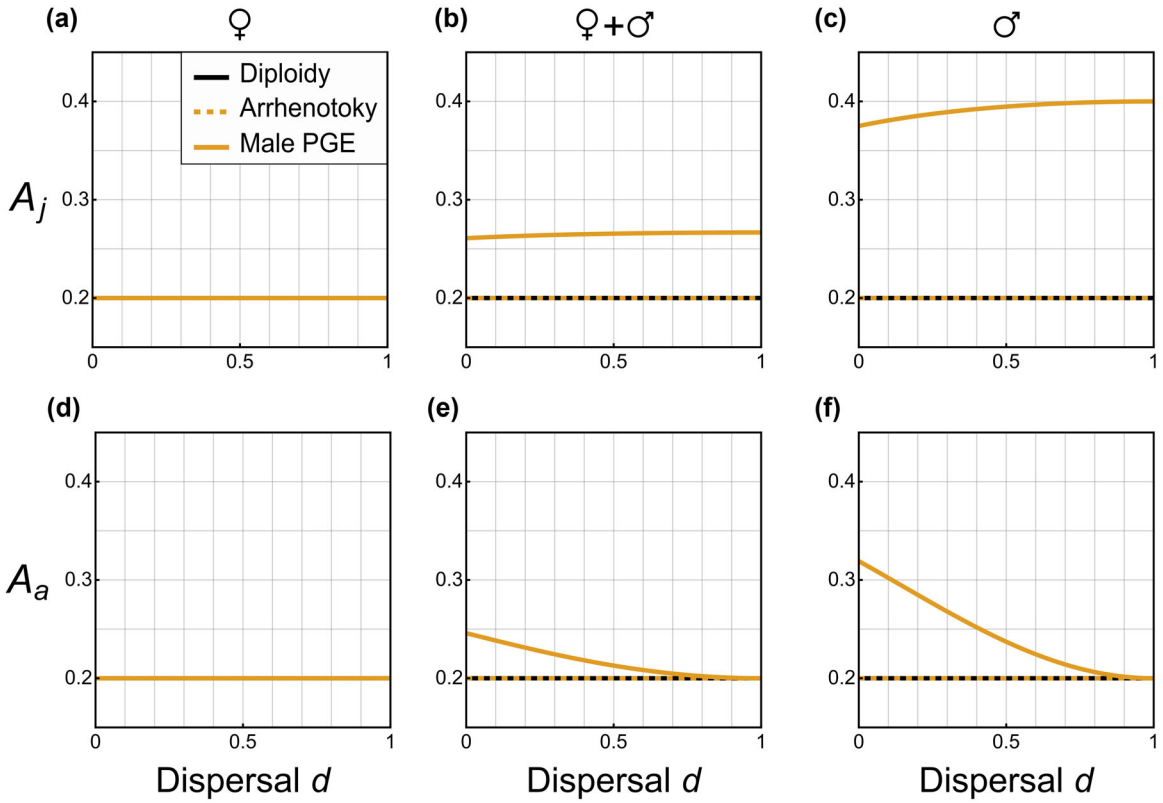

Figure 1. Dispersal modulates the potential for altruism (A) under paternal genome elimination (PGE), but not under diploidy or arrhenotoky, with the direction and magnitude of effect depending on when during the life cycle the behavior is expressed (a–c, juveniles A_j; d–f, adults A_a), and the sex of the actor expressing the behavior (a, d, exclusively females; b, e, both sexes; c, f, exclusively males). Across all panels $n = 5$. For the case of male PGE, we assume that there is equal expression from the maternal-origin and paternal-origin gene copies in males (i.e., $\tau = 1/2$). Explicit expressions for all these cases and extensions to sex-biased dispersal and patch size can be found in Supporting Information S6.

positive fecundity benefit shared across the individuals in the patch (i.e., $b_a > 0$), although other combinations of fitness effects are possible. We can then use these marginal fitness effects (in conjunction with the appropriate relatedness and reproductive-value coefficients) to calculate our conditions for increase (Supporting Information S6). We then rearrange these conditions into the form $c_t/b_t < A_t$, where A_t is the potential for altruism at time t in the life cycle ($t \in \{j,a\}$) (cf. Gardner 2010). With higher levels of A, it is less stringent for helping behaviours to increase, and more stringent for harming behaviours to increase. Further methodological details can be seen in Supporting Information S1–S6.

PGE and the Potential for Altruism

We begin by considering altruism enacted solely by females, that is, where the trait is exclusively expressed by females, although both males and females may be recipients of the behavior. For both juvenile and adult females, and for haploidy, diploidy, haplodiploidy (arrhenotoky), and PGE, we find that the potential for altruism is given by $A_t = 1/n$, where n is the number of male and female breeders on the patch, that is, the size of the demographic "bottleneck" that generates nonzero relatedness. That is, we recover the cancellation result as it pertains to female-only altruism under haploidy, diploidy, and haplodiploidy (Taylor 1992a; Johnstone and Cant 2008; Gardner 2010; Johnstone et al. 2012), and show that it also extends to female-only altruism under male PGE (Fig. 1a,d).

Next, we consider altruism enacted solely by males (Fig. 1c,f). For both juvenile and adult males, and for haploidy, diploidy, and haplodiploidy (arrhenotoky), we find that the potential for altruism is given by $A_t = 1/n$. That is, we recover the cancellation result as it pertains to male-only altruism under these three genetic systems (Johnstone and Cant 2008). In contrast, under male PGE, we find that the potential for altruism amongst juveniles is

$$A_j = \frac{2\left(4 - (1-d)^2\right)}{4n - (1-d)^2(n-1)}, \tag{1}$$

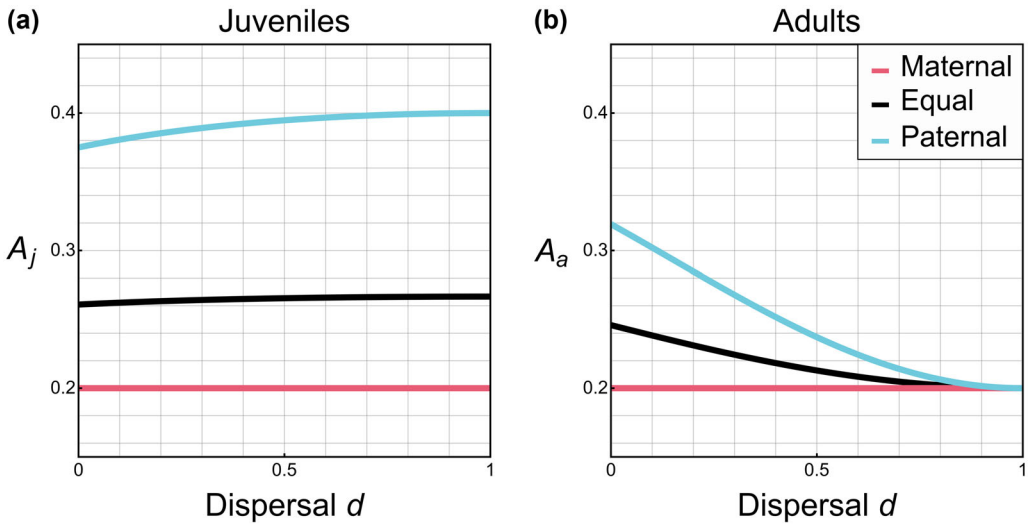

Figure 2. **The extent of expression from the paternal-origin genome modulates the potential for altruism (A) in males under PGE both at (a) juvenile (predispersal) A_j and (b) adult (postdispersal) A_a stages. With lowest altruism when there is exclusively maternal-origin expression in males ($\tau = 0$), higher potential for altruism with equal expression from those two gene copies ($\tau = 1/2$), and the highest potential for altruism when there is exclusively paternal-origin expression in males ($\tau = 1$). In both panels $n = 5$. Explicit expressions for all these cases can be seen in Supporting Information S6.**

and among adults it is

$$A_a = \frac{4n + (1-d)^2(3n+1) - (1-d)^4(n+1)}{4n^2 - (1-d)^2(n-5)n - (1-d)^4(n+1)}. \quad (2)$$

Inspecting these equations, we make several observations. First, the potential for altruism is higher under male PGE than the other investigated inheritance systems. Second, the potential for altruism is higher for males than for females. Third, unlike in the other cases, the potential for altruism depends upon the rate of dispersal. Fourth, the effect of dispersal is qualitatively different for juveniles and adults: among juveniles, increased dispersal is associated with an increase in the potential for altruism, whereas among adults increased dispersal is associated with a decrease in the potential for altruism. These patterns can be seen in Figure 1. In the case where altruistic behavior does not show sex-limited expression (Fig. 1d,e), then the altruism-promoting effect of PGE in relation to males leads to both males and females exhibiting a potential for altruism that is both higher than that predicted for haploid, diploid, and haplodiploid (arrhenotokous) genetic systems and also dependent upon the rate of dispersal (Fig. 1; Supporting Information S6).

These differences between PGE and arrhenotoky are, ultimately, due to the expression of the male paternal-origin genome. As this genome is not transmitted by its carrier, it has no direct fitness interests in the reproduction of that carrier, and thus is predisposed to altruism. We can show this by altering the influence that the paternal-origin genome has upon the male phenotype (Fig. 2; Supporting Information S4 and S6). This also allows us to explore some of the natural variation seen in the extent of male paternal genome expression (e.g., de la Filia et al. 2015). When the phenotype is exclusively controlled by maternal-origin genes, that is, solely the maternal-origin gene copy is expressed in males, the results coincide exactly with those for arrhenotoky, yielding $A_t = 1/n$ for both juveniles and adults. In contrast, when the phenotype is under the sole control of the paternal-origin genes, that is, solely the paternal-origin gene copy is expressed in males, then the potential for altruism is higher still, with the same qualitative pattern as reported above (Fig. 2). Thus, we can also see that, due to their different potentials for altruism, there is scope for strong intragenomic conflict between the maternal-origin and paternal-origin genomes in males (Burt and Trivers 2006; Gardner and Úbeda 2017). Full analytical expressions can be seen in Supporting Information S6, and the additional effects of sex-biased demography can be seen in Figures S2–S9.

Discussion

Here, we have shown that the unusual genetics of PGE, working in combination with population viscosity, is expected to drive distinct patterns of social behavior as compared to other genetic systems that have been investigated previously. This includes generally higher levels of altruistic behavior, with the extent of this dependent on the timing of the social behavior, sex of the actor, degree of paternal genome expression, and—notably—the rate of dispersal. These effects owe to the relative disincentive faced by a male's paternal-origin genome with respect to the pursuit of his personal reproductive success, on account of this portion of his genome not being transmitted to his offspring, and which

therefore makes him more inclined to altruistic behavior. These results indicate that various PGE groups may prove to be exceptional study systems with which to investigate the evolution of social behaviors, lending themselves to clear-cut within- and between-population comparative predictions concerning these factors that do not apply in more standard genetic settings.

Previously, much of the work unpicking the classic result that the evolutionarily favored level of altruism is invariant with respect to the rate of dispersal has been focused on ecology. This, as suggested above, may stem from Taylor's (1992a) thoroughness in covering the most common genetic systems—haploidy, diploidy, and haplodiploidy (arrhenotoky)—and showing that the same result obtains in all cases. However, recent results demonstrate that there are genetic systems wherein this invariance does not hold (Yeh and Gardner 2012; Hitchcock and Gardner 2021), with our results providing yet another example. Some of these systems, such as those featuring the zero-reproductive-value "zombies" investigated by Yeh and Gardner (2012), are likely rare in nature, with the closest approximations of this being the hermaphroditism of Icerya (Gardner and Ross 2011) and the androgenesis of corbicula clams, Saharan cypress, and *Bacillus* stick insects (Schwander and Oldroyd 2016). PGE, by contrast, is more common, having arisen independently in at least seven clades of arthropods, and thought to be in many thousands of species. Given the findings of the present analysis, it is worth re-examining some other unusual genetic systems that—even if rare—may provide other interesting exceptions to the invariance result. For example, species that exhibit somatic chimerism—such as Callitrichid monkeys (Haig 1999; Ross et al. 2007; Patten 2021), brown seaweeds (González and Santelices 2017), hydrozoans (Chang et al. 2018), and scleractinian corals (Puill-Stephan et al. 2009; Schweinsberg et al. 2015; Guerrini et al. 2021)—share some conceptual similarities to PGE, with individuals containing genes that may not be transmitted further, and thus may also be worth investigating, both theoretically and empirically, in the light of this work. Moreover, unusual systems such as PGE provide interesting test cases with which to enrich our understanding of how relatedness, reproductive value, and kin competition intersect to shape the evolution of various social behaviors. This may prove useful for when we move beyond the comforts of classic population genetics to try and understand the consequences of stranger, nongenetic inheritance systems (Bonduriansky and Day 2018).

Population viscosity is also particularly relevant for PGE species that—like other haplodiploid groups—often experience ecologies involving significant population subdivision, limited dispersal, and high levels of inbreeding (Hamilton 1967; Burt and Trivers 2006; Gardner and Ross 2014; Hitchcock et al. 2022). Although here we have focused on a generic life cycle to illustrate the difference in the potential for altruism between PGE and other inheritance systems, future modeling should incorporate more of the idiosyncratic life cycle features found in these groups, as well as the variation among them. Such details might include the timing of mating during the life cycle, the extent of generational overlap, and monogenic reproduction. These details will not only enrich the theory but will also enable more ecologically relevant models to be tailored to these particular groups.

The present analysis suggests that we may expect PGE species to display distinct patterns of social behavior. However, this is currently challenging to test as data on the social ecology of some of these groups remain relatively sparse. This is in part be due to technical issues, as many of these species are small, and often live in harder-to-view locations such as within soil or under bark. Nonetheless, there are some interesting instances of quite striking social behaviors. For example, since the 19th century, strange mass movements of the larvae of sciarid flies (primarily *Sciara militaris*) referred to as "armyworms" or "snakeworms" have been observed in Europe, North America, South America, and Asia (Sutou et al. 2011). Additionally, some groups have unusual mating behaviors, such as those described in globular springtails (*Deuterosminthurus bicinctus*) whereby males and females engage in a "push-and-pull" courtship ritual, followed by sperm transfer, and then competition between mates for spermatophore remains (Kozlowski and Aoxiang 2006). Alongside further study of particular social behaviors, groups such as the scale insects may be particularly amenable for comparative tests as to how mode of inheritance shapes social behavior, with this group spanning an extraordinary array of genetic systems, from diploidy and arrhenotoky, to male PGE and even hermaphroditism (Nur 1980; Ross et al. 2010; Mongue et al. 2021).

We have also shown that the asymmetric genetics of PGE generates strong sex differences in the potential for altruism, which may be associated with strong sex differences in social behavior and concomitant sex-specific morphologies. One interesting behavioral pattern that qualitatively aligns with our results is seen in the armored scales whereby male crawlers feed on exposed and dangerous leaves, whereas females feed in the more-protected crevices in the bark (Gill 1997; Normark 2004). This could be viewed as an altruistic behavior by juvenile males to alleviate kin competition, although this has also been suggested to be driven by matrilineally inherited endosymbionts (Normark 2004; Ross et al. 2010). In *Cystococcus* coccids (Eriococcidae), female crawlers are carried to new feeding sites by their older, alate, brothers, with a single male carrying as many as 13 female crawlers (Gullan and Cockburn 1986). This intersexual phoresy has also been suggested to occur in three other groups of gall-inhabiting coccoids: *Mangalorea*, *Gallacoccus*, and *Echinogalla* (Takagi 2001). The males of these gall-forming coccids also display some further intriguing features,

such as robust legs and elongate, sharp claws, and thus the male nymphs have been suggested to play a defensive role (Takagi 2007). Second-instar males have also been suggested to perform a similar defensive role in the genus *Rutherfordia* (Takagi 2021).

More generally, these results may be linked to the extreme sexual dimorphism observed in some of these groups (Gray 1954; Damon 2000; Palacios-Vargas and Castaño-Meneses 2009). Such sexual dimorphism may, in turn, also modulate conditions for social behaviors to evolve (e.g., sex-biased dispersal; Johnstone and Cant 2008; Gardner 2010; Johnstone et al. 2012; Supporting Information S6), and thus further modeling is needed to understand how these factors may coevolve with one another. For example, if in PGE species males evolve to be less competitive with their siblings than are females, or provide a defensive role for the nest, then this may shape the sex-allocation decisions of parents. This is conceptually similar to models that have investigated coevolution of sex-specific offspring helping and sex allocation (Gardner and Ross 2013; Davies et al. 2016). In addition, if such sex-specific strategies are favored, but sex-limited expression is not possible, then this may generate sexual antagonism, which is known to manifest differently in PGE species (Klein et al. 2021; Hitchcock et al. 2022) and may also be altered by sex-biased demographic processes (Flintham et al. 2021; Hitchcock et al. 2022), further altering evolutionary trajectories.

We have also considered how, within males, maternal-origin and paternal-origin genes may have very different potentials for altruism. This might be expected to lead to intense intragenomic conflicts of interest over a wide class of social traits, in addition to the conflicts that exist over transmission (Herrick and Seger 1999). Previously, Ross et al. (2011) investigated one such conflict, modeling how a paternal-origin-expressed male suicide trait may invade a population, generating a selection pressure for the silencing of the paternal genome from the maternal-origin genome. They suggest that this may be one explanation for the common pattern of paternal-genome heterochromatization seen in PGE groups. Given that we might expect strong intragenomic conflict between these two genomes over other social traits beyond suicide, then there may be further reasons to expect genomic imprinting (and potentially of both maternal-origin and paternal-origin genes). Furthermore, although not considered in the present analysis, we might expect parents to disagree with offspring over the social traits that they should express. In particular, mothers in PGE species may be expected to favor lower levels of altruism than the male paternal-origin genome in their sons, and thus they may be favored to silence this genome if possible. Moreover, if sons preferentially direct their altruism to female kin, then monogeny (seen in both sciarid flies and gall midges [Hodson and Ross 2021]) may be a further mechanism to reduce such altruistic behavior in sons. This array of intergenomic and intragenomic conflict of interests that PGE generates may provide an explanation for not only the remarkable diversity of genetic systems in these groups, but also the dynamic transitions between them (Ross et al. 2010).

ACKNOWLEDGMENTS

We thank R. Baird, V. Litzke, L. Ross, K. Stucky, and Z. Yang for helpful discussion, two anonymous reviewers for constructive feedback, and A. Douglas for the Scots translation. TJH is supported by a PhD scholarship funded by the School of Biology, University of St Andrews. AG is supported by a Natural Environment Research Council Independent Research Fellowship (grant no. NE/K009524/1) and a European Research Council Consolidator Grant (no. 771387).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

TJH and AG jointly designed the study. TJH performed the analysis. TJH and AG wrote the manuscript.

DATA ARCHIVING

There are no data to be archived.

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Associate Editor: Dr. B. Kuijper
Handling Editor: Dr. A. McAdam

Supporting Information

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

Supplementary Material

Supplementary Material for:
Paternal genome elimination promotes altruism in viscous populations

Thomas J. Hitchcock[1*] and Andy Gardner[1]

[1]School of Biology, University of St Andrews, St Andrews, UK

*Correspondence: th76@st-andrews.ac.uk

1 Life cycle

Here we analyse the following life-cycle, illustrated in Figure S1. This is a more general version than that described in the main text, allowing for various sexual asymmetries in ecology, such as dispersal and adult sex ratio. We assume that there is a infinite population subdivided into a large number of patches. It proceeds as so: (1) a large number of juveniles are born onto a patch, of which a proportion ρ are male and $1-\rho$ female. (2) Individuals then engage in a social behaviour z_{j} which modulates their survival to adulthood, which is S_{f} for females and S_{m} for males. (3) Individuals then disperse from their natal patch with sex-specific probabilities, d_{f} for females and d_{m} for males. (4) Post-dispersal, individuals compete for the n_{f} female and n_{m} male breeding spots on each patch, unsuccessful individuals die. (5) Adult individuals then engage in a second social behaviour z_{a} which modulates their fecundity F_{f} for females and F_{m} for males. After producing new juveniles, the adults on the patch die, and the life-cycle begins once more.

2 Fitness functions

In our model there two classes of individual, female and male, and four possible types of transition between these two classes (females through daughters, females through sons, males through daughters, males through sons). The absolute fitness of a parent of class $\mathbb{i}$ through production of class $\mathbb{j}$ offspring is written as $w_{\mathbb{i}\to\mathbb{j}}$. We census the population at phase (1) of the life cycle described above, and thus $w_{\mathbb{i}\to\mathbb{j}}$ refers to the absolute number of new individuals of class $\mathbb{j}$ in the next iteration of the life cycle to whom this focal individual is assigned parentage. The relative fitness of an individual is their absolute fitness through a particular route in the life cycle divided by the absolute fitness of an average individual through that same class transition. This can be written as:

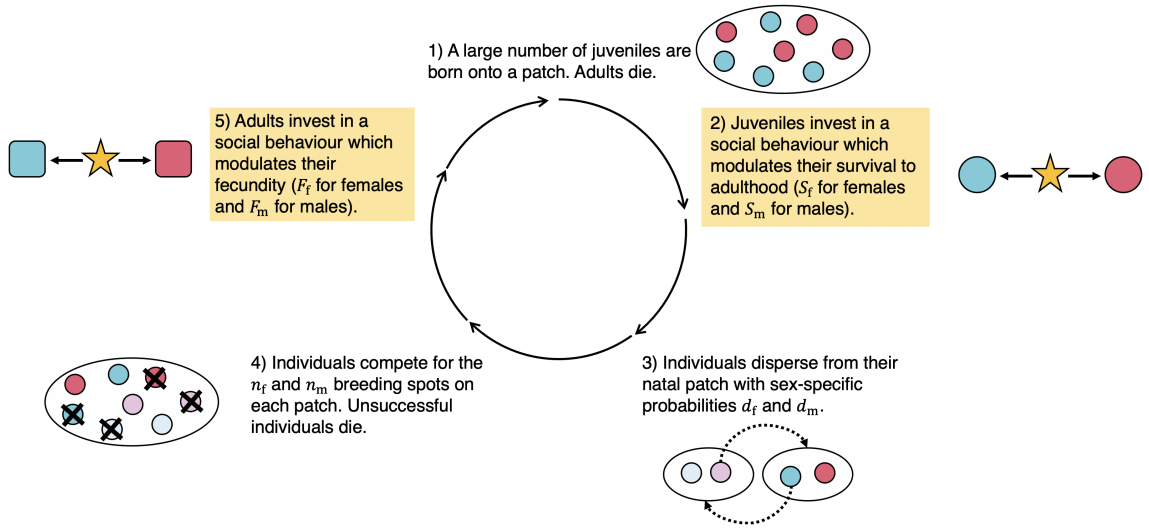

Figure S1: **Description of the key phases in the life-cycle.** These include: birth (1), juvenile social behaviour and survival (2), dispersal (3), competition for breeding spots (4), and adult social behaviour (5). The two phases highlighted in yellow represent the stages in which our two social behaviours analysed (z_j and z_a) occur.

$$W_{\mathbb{i}\to\mathbb{j}} = \frac{w_{\mathbb{i}\to\mathbb{j}}}{\overline{w}_{\mathbb{i}\to\mathbb{j}}} \tag{S1}$$

The absolute fitness of an individual of sex $\mathbb{i}$ through sex $\mathbb{j}$ offspring $w_{\mathbb{i}\to\mathbb{j}}$ in our life cycle is the product of: their probability of survival $S_{\mathbb{i}}$ (phase 2), the probability they obtain a breeding spot $\theta_{\mathbb{i}}$ (phase 3), and their fecundity $F_{\mathbb{i}}$ (phase 5). We can write these out as so:

$$w_{f\to f} = S_f \times \theta_f \times F_f(1-\rho) \tag{S2a}$$

$$w_{f\to m} = S_f \times \theta_f \times F_f\rho \tag{S2b}$$

$$w_{m\to f} = S_m \times \theta_m \times F_m(1-\rho) \tag{S2c}$$

$$w_{m\to m} = S_m \times \theta_m \times F_m\rho \tag{S2d}$$

A focal individual's survival is a function of both their own juvenile trait value $x_{\mathbb{i}j}$, and the trait value of their juvenile female y_{fj} and male social partners y_{mj}, e.g. a focal female's survival is $S_f\left(x_{fj}, y_{fj}, y_{mj}\right)$. A focal individual's fecundity is a function of their own adult trait value $x_{\mathbb{i}a}$ and the average female y_{fa} and male trait value y_{ma} in their focal patch (including themselves), e.g. a focal female's fecundity is $F_f\left(x_{fa}, y_{fa}, y_{ma}\right)$. We allow these social behaviours to be sex-limited in their expression, in these cases only the sex which expresses the trait will impact these phenotypes.

The probabilities that a focal female θ_f and a focal male θ_m obtain a breeding spot are not directly functions of the focal individual's trait value (i.e. competition is random with respect to phenotype), but instead is a function of the number of same sex competitors on their patch, which is determined by: the average fecundities of

the adult females and males on the focal patch in the previous generation $\hat{F}_\mathrm{f}$ and $\hat{F}_\mathrm{m}$, the average fecundities in the population $\overline{F}_\mathrm{f}$ and $\overline{F}_\mathrm{m}$, the average survival of same sex juveniles on the focal patch $\hat{S}_\mathrm{f}$ and $\hat{S}_\mathrm{m}$, and the survival probabilities of juveniles on the average patch in the population $\overline{S}_\mathrm{f}$ and $\overline{S}_\mathrm{m}$. This can be written out as so:

$$\theta_\mathrm{f} = \frac{(1-d_\mathrm{f})n_\mathrm{f}}{(1-d_\mathrm{f})n_\mathrm{f}\hat{F}_\mathrm{f}(1-\rho)\hat{S}_\mathrm{f} + d_\mathrm{f}n_\mathrm{f}\overline{F}_\mathrm{f}(1-\rho)\overline{S}_\mathrm{f}} + \frac{d_\mathrm{f}n_\mathrm{f}}{n_\mathrm{f}\overline{F}_\mathrm{f}(1-\rho)\overline{S}_\mathrm{f}} \tag{S3a}$$

$$\theta_\mathrm{m} = \frac{(1-d_\mathrm{m})n_\mathrm{m}}{(1-d_\mathrm{m})n_\mathrm{m}\hat{F}_\mathrm{m}\rho\hat{S}_\mathrm{m} + d_\mathrm{m}n_\mathrm{m}\overline{F}_\mathrm{m}\rho\overline{S}_\mathrm{m}} + \frac{d_\mathrm{m}n_\mathrm{m}}{n_\mathrm{m}\overline{F}_\mathrm{m}\rho\overline{S}_\mathrm{m}} \tag{S3b}$$

In addition, note the constraint that $n_\mathrm{f}\hat{F}_\mathrm{f} = n_\mathrm{m}\hat{F}_\mathrm{m}$ and $n_\mathrm{f}\overline{F}_\mathrm{f} = n_\mathrm{m}\overline{F}_\mathrm{m}$. We do not assume whether it is males or females who ultimately are the limiting factor upon reproduction and thus determine the fecundity of the patch (and population). We simply place the constraint that the total fecundity of males and females on each patch (and in the population) is equal. Subsequently, it is possible to interchange these fecundities in the fitness expressions. This is similar to the approach used by Johnstone and Cant (2008). Converting our expressions for absolute fitness to relative fitness, they become:

$$W_{\mathrm{f}\to\mathrm{f}} = \frac{w_{\mathrm{f}\to\mathrm{f}}}{\overline{w}_{\mathrm{f}\to\mathrm{f}}} = (1-d_\mathrm{f})\frac{S_\mathrm{f}F_\mathrm{f}}{(1-d_\mathrm{f})\hat{S}_\mathrm{f}\hat{F}_\mathrm{f} + d_\mathrm{f}\overline{S}_\mathrm{f}\overline{F}_\mathrm{f}} + d_\mathrm{f}\frac{S_\mathrm{f}F_\mathrm{f}}{\overline{S}_\mathrm{f}\overline{F}_\mathrm{f}} \tag{S4a}$$

$$W_{\mathrm{f}\to\mathrm{m}} = \frac{w_{\mathrm{f}\to\mathrm{m}}}{\overline{w}_{\mathrm{f}\to\mathrm{m}}} = (1-d_\mathrm{f})\frac{S_\mathrm{f}F_\mathrm{f}}{(1-d_\mathrm{f})\hat{S}_\mathrm{f}\hat{F}_\mathrm{f} + d_\mathrm{f}\overline{S}_\mathrm{f}\overline{F}_\mathrm{f}} + d_\mathrm{f}\frac{S_\mathrm{f}F_\mathrm{f}}{\overline{S}_\mathrm{f}\overline{F}_\mathrm{f}} \tag{S4b}$$

$$W_{\mathrm{m}\to\mathrm{f}} = \frac{w_{\mathrm{m}\to\mathrm{f}}}{\overline{w}_{\mathrm{m}\to\mathrm{f}}} = (1-d_\mathrm{m})\frac{S_\mathrm{m}F_\mathrm{m}}{(1-d_\mathrm{m})\hat{S}_\mathrm{m}\hat{F}_\mathrm{m} + d_\mathrm{m}\overline{S}_\mathrm{m}\overline{F}_\mathrm{m}} + d_\mathrm{m}\frac{S_\mathrm{m}F_\mathrm{m}}{\overline{S}_\mathrm{m}\overline{F}_\mathrm{m}} \tag{S4c}$$

$$W_{\mathrm{m}\to\mathrm{m}} = \frac{w_{\mathrm{m}\to\mathrm{m}}}{\overline{w}_{\mathrm{m}\to\mathrm{m}}} = (1-d_\mathrm{m})\frac{S_\mathrm{m}F_\mathrm{m}}{(1-d_\mathrm{m})\hat{S}_\mathrm{m}\hat{F}_\mathrm{m} + d_\mathrm{m}\overline{S}_\mathrm{m}\overline{F}_\mathrm{m}} + d_\mathrm{m}\frac{S_\mathrm{m}F_\mathrm{m}}{\overline{S}_\mathrm{m}\overline{F}_\mathrm{m}} \tag{S4d}$$

3 Marginal fitness effects

We now calculate the marginal fitness effects associated with a small change in the behaviour of different groups of individual upon our focal individuals. We notate the trait value of a focal individual of sex $\mathbb{k}$ and of locus $\mathbb{l}$, $x_{\mathbb{k}\mathbb{l}}$, and of the average group member as $y_{\mathbb{k}\mathbb{l}}$, and of the average group member in the parents generation as $Y_{\mathbb{k}\mathbb{l}}$. We make the following substitutions.

For our juvenile behaviours:

$$\frac{\partial(S_\mathrm{f}/\overline{S}_\mathrm{f})}{\partial x_\mathrm{fj}} = -c_\mathrm{fj} \tag{S5a}$$

$$\frac{\partial(S_\mathrm{m}/\overline{S}_\mathrm{m})}{\partial x_\mathrm{mj}} = -c_\mathrm{mj} \tag{S5b}$$

$$\frac{\partial(S_\mathrm{f}/\overline{S}_\mathrm{f})}{\partial y_\mathrm{fj}} = \frac{\partial(S_\mathrm{m}/\overline{S}_\mathrm{m})}{\partial y_\mathrm{fj}} = b_\mathrm{fj} \tag{S5c}$$

$$\frac{\partial(S_\mathrm{f}/\overline{S}_\mathrm{f})}{\partial y_\mathrm{mj}} = \frac{\partial(S_\mathrm{m}/\overline{S}_\mathrm{m})}{\partial y_\mathrm{mj}} = b_\mathrm{mj} \tag{S5d}$$

	∂x_{fj}	∂y_{fj}	∂x_{mj}	∂y_{mj}
∂W_{ff}	$-c_{\mathrm{fj}}$	$b_{\mathrm{fj}}-\kappa_{\mathrm{f}}(b_{\mathrm{fj}}-c_{\mathrm{fj}})$	0	$b_{\mathrm{mj}}(1-\kappa_{\mathrm{f}})$
∂W_{fm}	$-c_{\mathrm{fj}}$	$b_{\mathrm{fj}}-\kappa_{\mathrm{f}}(b_{\mathrm{fj}}-c_{\mathrm{fj}})$	0	$b_{\mathrm{mj}}(1-\kappa_{\mathrm{f}})$
∂W_{mf}	0	$b_{\mathrm{fj}}(1-\kappa_{\mathrm{m}})$	$-c_{\mathrm{mj}}$	$b_{\mathrm{mj}}-\kappa_{\mathrm{m}}(b_{\mathrm{mj}}-c_{\mathrm{mj}})$
∂W_{mm}	0	$b_{\mathrm{fj}}(1-\kappa_{\mathrm{m}})$	$-c_{\mathrm{mj}}$	$b_{\mathrm{mj}}-\kappa_{\mathrm{m}}(b_{\mathrm{mj}}-c_{\mathrm{mj}})$

Table S1: Marginal fitness effects for different genetic actors on self and social partners, for our juvenile trait affecting survival, where $\kappa_{\mathrm{f}}=(1-d_{\mathrm{f}})^2$ and $\kappa_{\mathrm{m}}=(1-d_{\mathrm{m}})^2$.

	∂x_{fa}	∂y_{fa}	∂Y_{fa}	∂x_{ma}	∂y_{ma}	∂Y_{ma}
∂W_{ff}	$-c_{\mathrm{fa}}$	b_{fa}	$-\kappa_{\mathrm{f}}(b_{\mathrm{fa}}-c_{\mathrm{fa}})$	0	$\frac{n_{\mathrm{m}}}{n_{\mathrm{f}}}(b_{\mathrm{ma}}-c_{\mathrm{ma}})$	$-\frac{n_{\mathrm{m}}}{n_{\mathrm{f}}}\kappa_{\mathrm{f}}(b_{\mathrm{ma}}-c_{\mathrm{ma}})$
∂W_{fm}	$-c_{\mathrm{fa}}$	b_{fa}	$-\kappa_{\mathrm{f}}(b_{\mathrm{fa}}-c_{\mathrm{fa}})$	0	$\frac{n_{\mathrm{m}}}{n_{\mathrm{f}}}(b_{\mathrm{ma}}-c_{\mathrm{ma}})$	$-\frac{n_{\mathrm{m}}}{n_{\mathrm{f}}}\kappa_{\mathrm{f}}(b_{\mathrm{ma}}-c_{\mathrm{ma}})$
∂W_{mf}	0	$\frac{n_{\mathrm{f}}}{n_{\mathrm{m}}}(b_{\mathrm{fa}}-c_{\mathrm{fa}})$	$-\frac{n_{\mathrm{f}}}{n_{\mathrm{m}}}\kappa_{\mathrm{m}}(b_{\mathrm{fa}}-c_{\mathrm{fa}})$	$-c_{\mathrm{ma}}$	b_{ma}	$-\kappa_{\mathrm{m}}(b_{\mathrm{ma}}-c_{\mathrm{ma}})$
∂W_{mm}	0	$\frac{n_{\mathrm{f}}}{n_{\mathrm{m}}}(b_{\mathrm{fa}}-c_{\mathrm{fa}})$	$-\frac{n_{\mathrm{f}}}{n_{\mathrm{m}}}\kappa_{\mathrm{m}}(b_{\mathrm{fa}}-c_{\mathrm{fa}})$	$-c_{\mathrm{ma}}$	b_{ma}	$-\kappa_{\mathrm{m}}(b_{\mathrm{ma}}-c_{\mathrm{ma}})$

Table S2: Marginal fitness effects for different genetic actors on self and social partners for our adult trait affecting fecundity, where $\kappa_{\mathrm{f}}=(1-d_{\mathrm{f}})^2$ and $\kappa_{\mathrm{m}}=(1-d_{\mathrm{m}})^2$.

And for our adult behaviours:

$$\frac{\partial(F_{\mathrm{f}}/\overline{F}_{\mathrm{f}})}{\partial x_{\mathrm{fa}}}=-c_{\mathrm{fa}} \tag{S6a}$$

$$\frac{\partial(F_{\mathrm{m}}/\overline{F}_{\mathrm{m}})}{\partial x_{\mathrm{ma}}}=-c_{\mathrm{ma}} \tag{S6b}$$

$$\frac{\partial(F_{\mathrm{f}}/\overline{F}_{\mathrm{f}})}{\partial y_{\mathrm{fa}}}=b_{\mathrm{fa}} \tag{S6c}$$

$$\frac{\partial(F_{\mathrm{m}}/\overline{F}_{\mathrm{m}})}{\partial y_{\mathrm{fa}}}=\frac{n_{\mathrm{f}}}{n_{\mathrm{m}}}(b_{\mathrm{fa}}-c_{\mathrm{fa}}) \tag{S6d}$$

$$\frac{\partial(F_{\mathrm{f}}/\overline{F}_{\mathrm{f}})}{\partial y_{\mathrm{ma}}}=\frac{n_{\mathrm{m}}}{n_{\mathrm{f}}}(b_{\mathrm{ma}}-c_{\mathrm{ma}}) \tag{S6e}$$

$$\frac{\partial(F_{\mathrm{m}}/\overline{F}_{\mathrm{m}})}{\partial y_{\mathrm{ma}}}=b_{\mathrm{ma}} \tag{S6f}$$

Making these substitutions, we can see the marginal fitness effects associated with a change in different social partners. In Table 1, we can see the marginal fitness effects associated with a change in the value of our juvenile social behaviours. In Table 2, we can see the marginal fitness effects associated with a change in the value of our adult social behaviours.

4 Consanguinities and relatedness coefficients

In order to calculate the relatedness coefficients between our different individuals, we first calculate the consanguinities between our different gene positions. These, in turn, are calculated by writing out recursions to

describe the probability of identity by descent between our different sets of gene positions in a neutral population. Assuming that the consanguinity coefficients have obtained their quasi-equilibrium values, such that the consanguinity between two gene positions in the next generation are equal to the consanguinity between those same two gene positions in this generation i.e. $Q'_{\mathbb{x},\mathbb{y}} = Q_{\mathbb{x},\mathbb{y}}$, then we may write out a system of simultaneous equations, which we can then solve in terms of our demographic parameters. Note that these are approximations of the true consanguinities, as genealogies may be altered by the action of selection, but is reasonable provided selection is weak (Frank, 1998; Rousset, 2004; Gardner et al., 2011).

Notation proceeds as follows. We notate the consanguinity between two genes sampled within an individual (with replacement) as $Q^i_{\mathbb{x},\mathbb{y}}$, between two juvenile individuals on a patch without replacement as $Q^p_{\mathbb{x},\mathbb{y}}$, and between a juvenile $\mathbb{x}$ in the current generation and an adult $\mathbb{y}$ on the same patch in the previous generation as $Q^v_{\mathbb{x},\mathbb{y}}$. For the haploid case, we have simply two types of gene position - males m and females f. In the diploid case, we have four gene positions: female maternal-origin genes $\mathrm{f_M}$, female paternal-origin genes $\mathrm{f_P}$, male maternal-origin genes $\mathrm{m_M}$, and male paternal-origin genes $\mathrm{m_P}$. So, for example, the probability of identity by descent between a female maternal-origin gene and a male paternal-origin gene from two juveniles on the same patch, would be written as $Q^p_{\mathrm{f_M},\mathrm{m_P}}$.

To describe the genetical system, we notate the probability that a maternal-origin gene was inherited from a maternal-origin gene α, and the probability a paternal-origin gene was inherited from a paternal-origin gene β. For the haploid case we have λ, which is the probability that a gene (in either a male or female) was inherited from a female. These parameters allows us to capture our various inheritance systems of interest in a single set of equations. For 'eumendelian' diploidy we have $\alpha = 1/2$,and $\beta = 1/2$, for arrhenotoky and male PGE we have $\alpha = 1/2$ and $\beta = 0$, and for paterothylotoky and female MGE we have $\alpha = 0$ and $\beta = 1/2$. For the haploid case, it allows us to explore the full range from full matrilineal inheritance $\lambda = 1$, to full patrilineal inheritance $\lambda = 0$.

To describe the mating system, we notate the probability that two juveniles born on the same patch share a mother $\mathscr{A}$, and the probability that two juveniles born on the same patch share a father $\mathscr{B}$. For our analysis we assume that $\mathscr{A} = 1/n_\mathrm{f}$ and $\mathscr{B} = 1/n_\mathrm{m}$. However, we write this out in the more general form here to draw similarities to other analyses (e.g. Gardner, 2010). The probability of inbreeding, i.e. the probability that two individuals born on the same patch mate, is given by $\phi = (1 - d_\mathrm{f})(1 - d_\mathrm{m})$.

Haploidy

Within individuals

In the haploid case, the probability that two gene copies sampled within an individual (with replacement) are identical by descent (IBD) is simply 1:

$$Q^i_{\mathrm{f,f}} = Q^i_{\mathrm{m,m}} = 1 \tag{S7a}$$

Between juvenile patchmates

The probability that two genes sampled in different juvenile patchmates are IBD is the probability that either they come from the same sex parent (λ^2 or $(1-\lambda)^2$), in which case they are IBD if they come from the same parent ($\mathscr{A}$ or $\mathscr{B}$), or if they come from different parents ($1-\mathscr{A}$ or $1-\mathscr{B}$) then they are IBD with the probability that those parents were natal to the patch and are IBD ($(1-d_\mathrm{f})^2 Q^p_{\mathrm{f,f}}$ or $(1-d_\mathrm{m})^2 Q^p_{\mathrm{m,m}}$). Alternatively, if they come from different sex parents, then they are IBD if those parents are both natal to the patch (ϕ), and were IBD as juveniles ($Q^p_{\mathrm{f,m}}$).

$$\begin{aligned} Q^p_{\mathrm{f,f}} = Q^p_{\mathrm{f,m}} = Q^p_{\mathrm{m,f}} = Q^p_{\mathrm{m,m}} = \\ \lambda\left(\lambda\left(\mathscr{A}Q^i_{\mathrm{f,f}} + (1-\mathscr{A})(1-d_\mathrm{f})^2 Q^p_{\mathrm{f,f}}\right) + (1-\lambda)\phi Q^p_{\mathrm{f,m}}\right) \\ + (1-\lambda)\left(\lambda\phi Q^p_{\mathrm{f,m}} + (1-\lambda)\left(\mathscr{B}Q^i_{\mathrm{m,m}} + (1-\mathscr{B})(1-d_\mathrm{m})^2 Q^p_{\mathrm{m,m}}\right)\right) \end{aligned} \tag{S8a}$$

Between generations

Genes sampled in a juvenile and an adult female are IBD if first the gene in the juvenile came from a female in the previous generation (λ), if so then either it came directly from that female ($\mathscr{A}$), or if it came from another female ($1-\mathscr{A}$), in which case they are IBD if those two females were both natal to the patch ($(1-d_\mathrm{f})^2$), and were IBD as juveniles ($Q^p_{\mathrm{f,f}}$). If the gene sampled in a juvenile came from a male ($1-\lambda$), then it would be the probability that the adult female and that father were both natal to the patch (ϕ), and were IBD as juveniles ($Q^p_{\mathrm{f,m}}$.) A similar logic can be used to calculate the consanguinity between a juvenile and an adult male.

$$Q^v_{\mathrm{f,f}} = Q^v_{\mathrm{m,f}} = \lambda\left(\mathscr{A}Q^i_{\mathrm{f,f}} + (1-\mathscr{A})(1-d_\mathrm{f})^2 Q^p_{\mathrm{f,f}}\right) + (1-\lambda)\phi Q^p_{\mathrm{f,m}} \tag{S9a}$$

$$Q^v_{\mathrm{f,m}} = Q^v_{\mathrm{m,m}} = \lambda\phi Q^p_{\mathrm{f,m}} + (1-\lambda)\left(\mathscr{B}Q^i_{\mathrm{m,m}} + (1-\mathscr{B})(1-d_\mathrm{m})^2 Q^p_{\mathrm{m,m}}\right) \tag{S9b}$$

Diploidy

The equations for diploidy follow a similar logic to those for haploidy, except we now have additional gene positions ($\mathrm{f_M}, \mathrm{f_P}, \mathrm{m_M}, \mathrm{m_P}$), and additional notation to describe the transmission genetics (α, β).

Within individuals

$$Q^i_{\mathrm{f_M,f_M}} = Q^i_{\mathrm{f_P,f_P}} = Q^i_{\mathrm{m_M,m_M}} = Q^i_{\mathrm{m_P,m_P}} = 1 \tag{S10a}$$

$$Q^i_{\mathrm{f_M,f_P}} = Q^i_{\mathrm{m_M,m_P}} = \alpha\left((1-\beta)\phi Q^p_{\mathrm{f_M,m_M}} + \beta\phi Q^p_{\mathrm{f_M,m_P}}\right) + (1-\alpha)\left((1-\beta)\phi Q^p_{\mathrm{f_P,m_M}} + \beta\phi Q^p_{\mathrm{f_P,m_P}}\right) \tag{S10b}$$

Between juvenile patchmates

$$\begin{aligned} Q^p_{\mathrm{f_M,f_M}} = \alpha\left(\alpha\left(\mathscr{A}Q^i_{\mathrm{f_M,f_M}} + (1-\mathscr{A})(1-d_\mathrm{f})^2 Q^p_{\mathrm{f_M,f_M}}\right) + (1-\alpha)\left(\mathscr{A}Q^i_{\mathrm{f_M,f_P}} + (1-\mathscr{A})(1-d_\mathrm{f})^2 Q^p_{\mathrm{f_M,f_P}}\right)\right) \\ + (1-\alpha)\left(\alpha\left(\mathscr{A}Q^i_{\mathrm{f_M,f_P}} + (1-\mathscr{A})(1-d_\mathrm{f})^2 Q^p_{\mathrm{f_M,f_P}}\right) + (1-\alpha)\left(\mathscr{A}Q^i_{\mathrm{f_P,f_P}} + (1-\mathscr{A})(1-d_\mathrm{f})^2 Q^p_{\mathrm{f_P,f_P}}\right)\right) \end{aligned} \tag{S11a}$$

$$Q^{p}_{\mathrm{f_M},\mathrm{f_P}} = \alpha\left((1-\beta)\phi Q^{p}_{\mathrm{f_M},\mathrm{m_M}} + \beta\phi Q^{p}_{\mathrm{f_M},\mathrm{m_P}}\right) + (1-\alpha)\left((1-\beta)\phi Q^{p}_{\mathrm{f_P},\mathrm{m_M}} + \beta\phi Q^{p}_{\mathrm{f_P},\mathrm{m_P}}\right) \tag{S11b}$$

$$Q^{p}_{\mathrm{f_P},\mathrm{f_P}} = (1-\beta)\left((1-\beta)\left(\mathscr{B}Q^{i}_{\mathrm{m_M},\mathrm{m_M}} + (1-\mathscr{B})(1-d_{\mathrm{m}})^2 Q^{p}_{\mathrm{m_M},\mathrm{m_M}}\right) + \beta\left(\mathscr{B}Q^{i}_{\mathrm{m_M},\mathrm{m_P}} + (1-\mathscr{B})(1-d_{\mathrm{m}})^2 Q^{p}_{\mathrm{m_M},\mathrm{m_P}}\right)\right) + \beta\left((1-\beta)\left(\mathscr{B}Q^{i}_{\mathrm{m_M},\mathrm{m_P}} + (1-\mathscr{B})(1-d_{\mathrm{m}})^2 Q^{p}_{\mathrm{m_M},\mathrm{m_P}}+\right) + \beta\left(\mathscr{B}Q^{i}_{\mathrm{m_P},\mathrm{m_P}} + (1-\mathscr{B})(1-d_{\mathrm{m}})^2 Q^{p}_{\mathrm{m_P},\mathrm{m_P}}\right)\right) \tag{S11c}$$

$$Q^{p}_{\mathrm{f_M},\mathrm{m_M}} = \alpha\left(\alpha\left(\mathscr{A}Q^{i}_{\mathrm{f_M},\mathrm{f_M}} + (1-\mathscr{A})(1-d_{\mathrm{f}})^2 Q^{p}_{\mathrm{f_M},\mathrm{f_M}}\right) + (1-\alpha)\left(\mathscr{A}Q^{i}_{\mathrm{f_M},\mathrm{f_P}} + (1-\mathscr{A})(1-d_{\mathrm{f}})^2 Q^{p}_{\mathrm{f_M},\mathrm{f_P}}\right)\right) + (1-\alpha)\left(\alpha\left(\mathscr{A}Q^{i}_{\mathrm{f_M},\mathrm{f_P}} + (1-\mathscr{A})(1-d_{\mathrm{f}})^2 Q^{p}_{\mathrm{f_M},\mathrm{f_P}}\right) + (1-\alpha)\left(\mathscr{A}Q^{i}_{\mathrm{f_P},\mathrm{f_P}} + (1-\mathscr{A})(1-d_{\mathrm{f}})^2 Q^{p}_{\mathrm{f_P},\mathrm{f_P}}\right)\right) \tag{S11d}$$

$$Q^{p}_{\mathrm{f_M},\mathrm{m_P}} = \alpha\left((1-\beta)\phi Q^{p}_{\mathrm{f_M},\mathrm{m_M}} + \beta\phi Q^{p}_{\mathrm{f_M},\mathrm{m_P}}\right) + (1-\alpha)\left((1-\beta)\phi Q^{p}_{\mathrm{f_P},\mathrm{m_M}} + \beta\phi Q^{p}_{\mathrm{f_P},\mathrm{m_P}}\right) \tag{S11e}$$

$$Q^{p}_{\mathrm{f_P},\mathrm{m_P}} = (1-\beta)\left((1-\beta)\left(\mathscr{B}Q^{i}_{\mathrm{m_M},\mathrm{m_M}} + (1-\mathscr{B})(1-d_{\mathrm{m}})^2 Q^{p}_{\mathrm{m_M},\mathrm{m_M}}\right) + \beta\left(\mathscr{B}Q^{i}_{\mathrm{m_M},\mathrm{m_P}} + (1-\mathscr{B})(1-d_{\mathrm{m}})^2 Q^{p}_{\mathrm{m_M},\mathrm{m_P}}\right)\right) + \beta\left((1-\beta)\left(\mathscr{B}Q^{i}_{\mathrm{m_M},\mathrm{m_P}} + (1-\mathscr{B})(1-d_{\mathrm{m}})^2 Q^{p}_{\mathrm{m_M},\mathrm{m_P}}\right) + \beta\left(\mathscr{B}Q^{i}_{\mathrm{m_P},\mathrm{m_P}} + (1-\mathscr{B})(1-d_{\mathrm{m}})^2 Q^{p}_{\mathrm{m_P},\mathrm{m_P}}\right)\right) \tag{S11f}$$

$$Q^{p}_{\mathrm{m_M},\mathrm{m_M}} = \alpha\left(\alpha\left(\mathscr{A}Q^{i}_{\mathrm{f_M},\mathrm{f_M}} + (1-\mathscr{A})(1-d_{\mathrm{f}})^2 Q^{p}_{\mathrm{f_M},\mathrm{f_M}}\right) + (1-\alpha)\left(\mathscr{A}Q^{i}_{\mathrm{f_M},\mathrm{f_P}} + (1-\mathscr{A})(1-d_{\mathrm{f}})^2 Q^{p}_{\mathrm{f_M},\mathrm{f_P}}\right)\right) + (1-\alpha)\left(\alpha\left(\mathscr{A}Q^{i}_{\mathrm{f_M},\mathrm{f_P}} + (1-\mathscr{A})(1-d_{\mathrm{f}})^2 Q^{p}_{\mathrm{f_M},\mathrm{f_P}}\right) + (1-\alpha)\left(\mathscr{A}Q^{i}_{\mathrm{f_P},\mathrm{f_P}} + (1-\mathscr{A})(1-d_{\mathrm{f}})^2 Q^{p}_{\mathrm{f_P},\mathrm{f_P}}\right)\right) \tag{S11g}$$

$$Q^{p}_{\mathrm{m_M},\mathrm{m_P}} = \alpha\left((1-\beta)\phi Q^{p}_{\mathrm{f_M},\mathrm{m_M}} + \beta\phi Q^{p}_{\mathrm{f_M},\mathrm{m_P}}\right) + (1-\alpha)\left((1-\beta)\phi Q^{p}_{\mathrm{f_P},\mathrm{m_M}} + \beta\phi Q^{p}_{\mathrm{f_P},\mathrm{m_P}}\right) \tag{S11h}$$

$$Q^{p}_{\mathrm{m_P},\mathrm{m_P}} = (1-\beta)\left((1-\beta)\left(\mathscr{B}Q^{i}_{\mathrm{m_M},\mathrm{m_M}} + (1-\mathscr{B})(1-d_{\mathrm{m}})^2 Q^{p}_{\mathrm{m_M},\mathrm{m_M}}\right) + \beta\left(\mathscr{B}Q^{i}_{\mathrm{m_M},\mathrm{m_P}} + (1-\mathscr{B})(1-d_{\mathrm{m}})^2 Q^{p}_{\mathrm{m_M},\mathrm{m_P}}\right)\right) + \beta\left((1-\beta)\left(\mathscr{B}Q^{i}_{\mathrm{m_M},\mathrm{m_P}} + (1-\mathscr{B})(1-d_{\mathrm{m}})^2 Q^{p}_{\mathrm{m_M},\mathrm{m_P}}+\right) + \beta\left(\mathscr{B}Q^{i}_{\mathrm{m_P},\mathrm{m_P}} + (1-\mathscr{B})(1-d_{\mathrm{m}})^2 Q^{p}_{\mathrm{m_P},\mathrm{m_P}}\right)\right) \tag{S11i}$$

Between generations

$$Q^{v}_{\mathrm{f_M},\mathrm{f_M}} = \alpha\left(\mathscr{A}Q^{i}_{\mathrm{f_M},\mathrm{f_M}} + (1-\mathscr{A})(1-d_{\mathrm{f}})^2 Q^{p}_{\mathrm{f_M},\mathrm{f_M}}\right) + (1-\alpha)\left(\mathscr{A}Q^{i}_{\mathrm{f_M},\mathrm{f_P}} + (1-\mathscr{A})(1-d_{\mathrm{f}})^2 Q^{p}_{\mathrm{f_M},\mathrm{f_P}}\right) \tag{S12a}$$

$$Q^{v}_{\mathrm{f_M},\mathrm{f_P}} = \alpha\left(\mathscr{A}Q^{i}_{\mathrm{f_M},\mathrm{f_P}} + (1-\mathscr{A})(1-d_{\mathrm{f}})^2 Q^{p}_{\mathrm{f_M},\mathrm{f_P}}\right) + (1-\alpha)\left(\mathscr{A}Q^{i}_{\mathrm{f_P},\mathrm{f_P}} + (1-\mathscr{A})(1-d_{\mathrm{f}})^2 Q^{p}_{\mathrm{f_P},\mathrm{f_P}}\right) \tag{S12b}$$

$$Q^{v}_{\mathrm{f_M},\mathrm{m_M}} = \alpha\phi Q^{p}_{\mathrm{f_M},\mathrm{m_M}} + (1-\alpha)\phi Q^{p}_{\mathrm{f_P},\mathrm{m_M}} \tag{S12c}$$

$$Q^{v}_{\mathrm{f_M},\mathrm{m_P}} = \alpha\phi Q^{p}_{\mathrm{f_M},\mathrm{m_P}} + (1-\alpha)\phi Q^{p}_{\mathrm{f_P},\mathrm{m_P}} \tag{S12d}$$

$$Q^{v}_{\mathrm{f_P},\mathrm{f_M}} = (1-\beta)\phi Q^{p}_{\mathrm{f_M},\mathrm{m_M}} + \beta\phi Q^{p}_{\mathrm{f_M},\mathrm{m_P}} \tag{S13a}$$

$$Q^{v}_{\mathrm{f_P},\mathrm{f_P}} = (1-\beta)\phi Q^{p}_{\mathrm{f_P},\mathrm{m_M}} + \beta\phi Q^{p}_{\mathrm{m_P},\mathrm{m_P}} \tag{S13b}$$

$$Q^{v}_{\mathrm{f_P},\mathrm{m_M}} = (1-\beta)\left(\mathscr{B}Q^{i}_{\mathrm{m_M},\mathrm{m_M}} + (1-\mathscr{B})(1-d_{\mathrm{m}})^2 Q^{p}_{\mathrm{m_M},\mathrm{m_M}}\right) + \beta\left(\mathscr{B}Q^{i}_{\mathrm{m_M},\mathrm{m_P}} + (1-\mathscr{B})(1-d_{\mathrm{m}})^2 Q^{p}_{\mathrm{m_M},\mathrm{m_P}}\right) \tag{S13c}$$

$$Q^{v}_{\mathrm{f_P},\mathrm{m_P}} = (1-\beta)\left(\mathscr{B}Q^{i}_{\mathrm{m_M},\mathrm{m_P}} + (1-\mathscr{B})(1-d_{\mathrm{m}})^2 Q^{p}_{\mathrm{m_M},\mathrm{m_P}}\right) + \beta\left(\mathscr{B}Q^{i}_{\mathrm{m_P},\mathrm{m_P}} + (1-\mathscr{B})(1-d_{\mathrm{m}})^2 Q^{p}_{\mathrm{m_P},\mathrm{m_P}}\right) \tag{S13d}$$

Relatedness coefficients

We can now calculate the relatedness coefficients as a weighted sum of the above consanguinity coefficients. Such weightings are necessary in this case because - with paternal-genome elimination - not all of the genes within an individual have the same prospects going forward. As we are performing a personal fitness analysis, then the required relatedness coefficients $r_{\mathbb{x},\mathbb{y}}$ describe the correlation between a focal individual's transmitted breeding value, which we denote $g_{\mathbb{x}}$, and the somatic breeding value of their social partners (including themselves), which we denote $G_{\mathbb{y}}$. Thus, the consanguinities between the gene copies within an individual to those in their social partners must be weighted in proportion to their contribution to the transmitted breeding value. Note, however, that these relatedness coefficients are distinct from those used in an inclusive fitness analysis (see Frank, 1998, Chapter 4), where instead relatedness is the correlation between a focal individual's somatic breeding value and their social partners' transmitted breeding value.

Similar to above, we denote the somatic breeding value of our focal individual G^i, the somatic breeding value of a juvenile individual on the focal patch as G^p, the somatic breeding value of an adult individual on the focal patch (including oneself) as G^q, and the somatic breeding value of an adult individual in the focal patch in the previous generation as G^v.

Earlier, we denoted the probability that a maternal-origin gene came from a maternal-origin gene α, and similarly we denoted the probability that a paternal-origin gene came from a paternal-origin gene β. Let the contribution of a female's maternal-origin gene to her transmitted breeding value be $\hat{\alpha}$, and the contribution of a male's paternal-origin gene to his transmitted breeding value be $\hat{\beta}$. In the case of this model, as the probability that maternal-origin gene came from a maternal-origin gene is α and the probability it comes from a paternal-origin gene $1-\alpha$, then the contribution that the maternal-origin makes to the transmitted breeding value of a female is simply $\hat{\alpha} = \alpha$, and similarly for the contribution of the paternal-origin gene to the transmitted breeding value of a male $\hat{\beta} = \beta$.

To allow for differential contributions to the somatic breeding value (i.e. the expressed phenotype), we denote σ to be the fraction of a female's somatic breeding value that comes from the her maternal-origin gene copy, and τ to be the fraction of a male's somatic breeding value that comes from his paternal-origin gene copy. For example, in the case of paternal genome elimination $\alpha = 1/2, \beta = 0$, if all gene copies were expressed then $\sigma = 1/2, \tau = 1/2$, whilst if the male paternal genome is silenced then $\sigma = 1/2, \tau = 0$, and if the male maternal genome is silenced then $\sigma = 1/2, \tau = 1$. These two parameters thus allow us to manipulate the degree of "control" that the maternal-origin and paternal-origin genes exert over the phenotype in females and males, biologically this would most likely arise from parent-of-origin specific gene expression, e.g. imprinting. Moreover, these tools allows us to investigate genetic systems such as classical haplodiploidy (e.g. arrhenotoky) within a diploid genetic system, by ignoring the contribution of the paternal-origin genome in males to the phenotype (i.e. by setting $\tau = 0$). For arrhenotoky and pareothylotoky, we additionally assume $\sigma = 1/2, \tau = 0$ and $\sigma = 0, \tau = 1/2$ respectively. For standard diploid we assume $\sigma = 1/2, \tau = 1/2$.

Haploidy

Within individuals

$$\frac{\mathrm{d}G^i_{\mathrm{f}}}{\mathrm{d}g_{\mathrm{f}}} = r^i_{\mathrm{f,f}} = Q^i_{\mathrm{f,f}} \tag{S14a}$$

$$\frac{\mathrm{d}G^i_{\mathrm{m}}}{\mathrm{d}g_{\mathrm{m}}} = r^i_{\mathrm{m,m}} = Q^i_{\mathrm{m,m}} \tag{S14b}$$

Between juvenile patchmates

$$\frac{\mathrm{d}G^p_{\mathrm{f}}}{\mathrm{d}g_{\mathrm{f}}} = r^p_{\mathrm{f,f}} = Q^p_{\mathrm{f,f}} \tag{S15a}$$

$$\frac{\mathrm{d}G^p_{\mathrm{m}}}{\mathrm{d}g_{\mathrm{f}}} = r^p_{\mathrm{f,m}} = Q^p_{\mathrm{f,m}} \tag{S15b}$$

$$\frac{\mathrm{d}G^p_{\mathrm{f}}}{\mathrm{d}g_{\mathrm{m}}} = r^p_{\mathrm{m,f}} = Q^p_{\mathrm{f,m}} \tag{S15c}$$

$$\frac{\mathrm{d}G^p_{\mathrm{m}}}{\mathrm{d}g_{\mathrm{m}}} = r^p_{\mathrm{m,m}} = Q^p_{\mathrm{m,m}} \tag{S15d}$$

Between adult patchmates

For the adults on a patch, we use whole group relatedness - i.e. sampling without replacement. The relatedness between two adult females on a patch $r^q_{\mathrm{f,f}}$, is then equal to the probability that the same individual is sampled twice $(1/n_{\mathrm{f}})$ multiplied by their relatedness to self $r^i_{\mathrm{f,f}}$, and the probability two different adults are sampled $((n_{\mathrm{f}}-1)/n_{\mathrm{f}})$, multiplied by the probability that they both did not disperse $(1-d_{\mathrm{f}})^2$, and then multiplied by the relatedness between two juvenile females $r^p_{\mathrm{f,f}}$. We can use this same approach to calculate the relatedness between other pairs of adults $(r^q_{\mathrm{f,m}}, r^q_{\mathrm{m,f}}, r^q_{\mathrm{m,m}})$.

$$\frac{\mathrm{d}G^q_{\mathrm{f}}}{\mathrm{d}g_{\mathrm{f}}} = r^q_{\mathrm{f,f}} = \left(\frac{1}{n_{\mathrm{f}}}\right) r^i_{\mathrm{f,f}} + \left(\frac{n_{\mathrm{f}}-1}{n_{\mathrm{f}}}\right)(1-d_{\mathrm{f}})^2 r^p_{\mathrm{f,f}} \tag{S16a}$$

$$\frac{\mathrm{d}G_{\mathrm{m}}^{q}}{\mathrm{d}g_{\mathrm{f}}} = r_{\mathrm{f,m}}^{q} = \phi r_{\mathrm{f,m}}^{p} \tag{S16b}$$

$$\frac{\mathrm{d}G_{\mathrm{f}}^{q}}{\mathrm{d}g_{\mathrm{m}}} = r_{\mathrm{m,f}}^{q} = \phi r_{\mathrm{m,f}}^{p} \tag{S16c}$$

$$\frac{\mathrm{d}G_{\mathrm{m}}^{q}}{\mathrm{d}g_{\mathrm{m}}} = r_{\mathrm{m,m}}^{q} = \left(\frac{1}{n_{\mathrm{m}}}\right) r_{\mathrm{m,m}}^{i} + \left(\frac{n_{\mathrm{m}}-1}{n_{\mathrm{m}}}\right)(1-d_{\mathrm{m}})^{2} r_{\mathrm{m,m}}^{p} \tag{S16d}$$

Between juveniles and the adults in their patch in the previous generation

$$\frac{\mathrm{d}G_{\mathrm{f}}^{v}}{\mathrm{d}g_{\mathrm{f}}} = r_{\mathrm{f,f}}^{v} = Q_{\mathrm{f,f}}^{v} \tag{S17a}$$

$$\frac{\mathrm{d}G_{\mathrm{m}}^{v}}{\mathrm{d}g_{\mathrm{f}}} = r_{\mathrm{f,m}}^{v} = Q_{\mathrm{f,m}}^{v} \tag{S17b}$$

$$\frac{\mathrm{d}G_{\mathrm{f}}^{v}}{\mathrm{d}g_{\mathrm{m}}} = r_{\mathrm{m,f}}^{v} = Q_{\mathrm{f,m}}^{v} \tag{S17c}$$

$$\frac{\mathrm{d}G_{\mathrm{m}}^{v}}{\mathrm{d}g_{\mathrm{m}}} = r_{\mathrm{m,m}}^{v} = Q_{\mathrm{m,m}}^{v} \tag{S17d}$$

Diploidy

Within individuals

$$\frac{\mathrm{d}G_{\mathrm{f}}^{i}}{\mathrm{d}g_{\mathrm{f}}} = r_{\mathrm{f,f}}^{i} = \sigma\left(\alpha Q_{\mathrm{f_M,f_M}}^{i} + (1-\alpha) Q_{\mathrm{f_M,f_P}}^{i}\right) + (1-\sigma)\left(\alpha Q_{\mathrm{f_M,f_P}}^{i} + (1-\alpha) Q_{\mathrm{f_P,f_P}}^{i}\right) \tag{S18a}$$

$$\frac{\mathrm{d}G_{\mathrm{m}}^{i}}{\mathrm{d}g_{\mathrm{m}}} = r_{\mathrm{m,m}}^{i} = (1-\tau)\left((1-\beta) Q_{\mathrm{m_M,m_M}}^{i} + \beta Q_{\mathrm{m_M,m_P}}^{i}\right) + \tau\left((1-\beta) Q_{\mathrm{m_M,m_P}}^{i} + \beta Q_{\mathrm{m_P,m_P}}^{i}\right) \tag{S18b}$$

Between juvenile patchmates

$$\frac{\mathrm{d}G_{\mathrm{f}}^{p}}{\mathrm{d}g_{\mathrm{f}}} = r_{\mathrm{f,f}}^{p} = \sigma\left(\alpha Q_{\mathrm{f_M,f_M}}^{p} + (1-\alpha) Q_{\mathrm{f_M,f_P}}^{p}\right) + (1-\sigma)\left(\alpha Q_{\mathrm{f_M,f_P}}^{p} + (1-\alpha) Q_{\mathrm{f_P,f_P}}^{p}\right) \tag{S19a}$$

$$\frac{\mathrm{d}G_{\mathrm{m}}^{p}}{\mathrm{d}g_{\mathrm{f}}} = r_{\mathrm{f,m}}^{p} = (1-\tau)\left(\alpha Q_{\mathrm{f_M,m_M}}^{p} + (1-\alpha) Q_{\mathrm{f_p,m_M}}^{p}\right) + \tau\left(\alpha Q_{\mathrm{f_M,m_P}}^{p} + (1-\alpha) Q_{\mathrm{f_P,m_P}}^{p}\right) \tag{S19b}$$

$$\frac{\mathrm{d}G_{\mathrm{f}}^{p}}{\mathrm{d}g_{\mathrm{m}}} = r_{\mathrm{m,f}}^{p} = \sigma\left((1-\beta) Q_{\mathrm{f_M,m_M}}^{p} + \beta Q_{\mathrm{f_M,m_P}}^{p}\right) + (1-\sigma)\left((1-\beta) Q_{\mathrm{f_P,m_M}}^{p} + \beta Q_{\mathrm{f_P,m_P}}^{p}\right) \tag{S19c}$$

$$\frac{\mathrm{d}G_{\mathrm{m}}^{p}}{\mathrm{d}g_{\mathrm{m}}} = r_{\mathrm{m,m}}^{p} = (1-\tau)\left((1-\beta) Q_{\mathrm{m_M,m_M}}^{p} + \beta Q_{\mathrm{m_M,m_P}}^{p}\right) + \tau\left((1-\beta) Q_{\mathrm{m_M,m_P}}^{p} + \beta Q_{\mathrm{m_P,m_P}}^{p}\right) \tag{S19d}$$

Between adult patchmates

$$\frac{\mathrm{d}G_{\mathrm{f}}^{q}}{\mathrm{d}g_{\mathrm{f}}} = r_{\mathrm{f,f}}^{q} = \left(\frac{1}{n_{\mathrm{f}}}\right) r_{\mathrm{f,f}}^{i} + \left(\frac{n_{\mathrm{f}}-1}{n_{\mathrm{f}}}\right)(1-d_{\mathrm{f}})^{2} r_{\mathrm{f,f}}^{p} \tag{S20a}$$

$$\frac{\mathrm{d}G^q_{\mathrm{m}}}{\mathrm{d}g_{\mathrm{f}}} = r^q_{\mathrm{f,m}} = \phi r^p_{\mathrm{f,m}} \tag{S20b}$$

$$\frac{\mathrm{d}G^q_{\mathrm{f}}}{\mathrm{d}g_{\mathrm{m}}} = r^q_{\mathrm{m,f}} = \phi r^p_{\mathrm{m,f}} \tag{S20c}$$

$$\frac{\mathrm{d}G^q_{\mathrm{m}}}{\mathrm{d}g_{\mathrm{m}}} = r^q_{\mathrm{m,m}} = \left(\frac{1}{n_{\mathrm{m}}}\right) r^i_{\mathrm{m,m}} + \left(\frac{n_{\mathrm{m}}-1}{n_{\mathrm{m}}}\right)(1-d_{\mathrm{m}})^2 r^p_{\mathrm{m,m}} \tag{S20d}$$

Between juveniles and the adults in their patch in the previous generation

$$\frac{\mathrm{d}G^v_{\mathrm{f}}}{\mathrm{d}g_{\mathrm{f}}} = r^v_{\mathrm{f,f}} = \sigma\left(\alpha Q^v_{\mathrm{f_M,f_M}} + (1-\alpha)Q^v_{\mathrm{f_M,f_P}}\right) + (1-\sigma)\left(\alpha Q^v_{\mathrm{f_M,f_P}} + (1-\alpha)Q^v_{\mathrm{f_P,f_P}}\right) \tag{S21a}$$

$$\frac{\mathrm{d}G^v_{\mathrm{m}}}{\mathrm{d}g_{\mathrm{f}}} = r^v_{\mathrm{f,m}} = (1-\tau)\left(\alpha Q^v_{\mathrm{f_M,m_M}} + (1-\alpha)Q^v_{\mathrm{f_P,m_M}}\right) + \tau\left(\alpha Q^v_{\mathrm{f_M,m_P}} + (1-\alpha)Q^v_{\mathrm{f_P,m_P}}\right) \tag{S21b}$$

$$\frac{\mathrm{d}G^v_{\mathrm{f}}}{\mathrm{d}g_{\mathrm{m}}} = r^v_{\mathrm{m,f}} = \sigma\left((1-\beta)Q^v_{\mathrm{f_M,m_M}} + \beta Q^v_{\mathrm{f_M,m_P}}\right) + (1-\sigma)\left((1-\beta)Q^v_{\mathrm{f_P,m_M}} + \beta Q^v_{\mathrm{f_P,m_P}}\right) \tag{S21c}$$

$$\frac{\mathrm{d}G^v_{\mathrm{m}}}{\mathrm{d}g_{\mathrm{m}}} = r^v_{\mathrm{m,m}} = (1-\tau)\left((1-\beta)Q^v_{\mathrm{m_M,m_M}} + \beta Q^v_{\mathrm{m_M,m_P}}\right) + \tau\left((1-\beta)Q^v_{\mathrm{m_M,m_P}} + \beta Q^v_{\mathrm{m_P,m_P}}\right) \tag{S21d}$$

5 Reproductive values

Reproductive value captures the asymptotic contribution that a particular class or individual makes to the ancestry of the population, thus providing a weighting of the relative importance of selection on that individual, or in that class of individuals (Fisher, 1999; Taylor, 1990; Grafen, 2006). We can compute the class reproductive values as so, let $\wp_{\mathbb{i}\leftarrow\mathbb{j}}$ be the probability that the transmitted breeding value of randomly sampled individual of class $\mathbb{i}$ came from class $\mathbb{j}$ in the previous time point. We can then write this out as a gene flow matrix T:

$$T = \begin{pmatrix} \wp_{\mathrm{f}\leftarrow\mathrm{f}} & \wp_{\mathrm{f}\leftarrow\mathrm{m}} \\ \wp_{\mathrm{m}\leftarrow\mathrm{f}} & \wp_{\mathrm{m}\leftarrow\mathrm{m}} \end{pmatrix} \tag{S22}$$

The dominant left eigenvector associated with the dominant eigenvalue of this matrix gives us the class reproductive values of males v_{m} and females v_{f}. Note that as this is a Markov matrix, the dominant eigenvalue will be 1, hence, we can solve the following equation to get our vector of class reproductive values.

$$\begin{pmatrix} v_{\mathrm{f}} & v_{\mathrm{m}} \end{pmatrix} = \begin{pmatrix} v_{\mathrm{f}} & v_{\mathrm{m}} \end{pmatrix} \begin{pmatrix} \wp_{\mathrm{f}\leftarrow\mathrm{f}} & \wp_{\mathrm{f}\leftarrow\mathrm{m}} \\ \wp_{\mathrm{m}\leftarrow\mathrm{f}} & \wp_{\mathrm{m}\leftarrow\mathrm{m}} \end{pmatrix} \tag{S23}$$

These class reproductive values provide the weights on allele frequency changes within classes, however, we may also wish to describe the relative importance of selection on the different types of transition between classes (Hamilton, 1966; Hitchcock and Gardner, 2020), i.e. on females reproduction through sons, male reproduction through daughters, or through female survival to females, etc. These weights are also referred to as elasticities in demographic analysis (de Kroon et al., 1986; Caswell, 2000; Bienvenu and Legendre, 2015). We write out the value of these different transitions by writing out the value of the class, and the probability that

a gene sampled in that class passed through a particular route in the previous generation. The reproductive value of the transition from class $\mathbb{i}$ to class $\mathbb{j}$ can be written as:

$$v_{\mathbb{i}\to\mathbb{j}} = \wp_{\mathbb{j}\leftarrow\mathbb{i}}\, v_{\mathbb{j}} \tag{S24}$$

Haploidy

In the case of haploidy, the probability that an individual's transmitted breeding value came from their mother in the previous generation is λ, and the probability it came from their father is $1-\lambda$. Thus our transition matrix becomes:

$$T = \begin{pmatrix} \lambda & 1-\lambda \\ \lambda & 1-\lambda \end{pmatrix} \tag{S25}$$

And thus once normalised ($\sum_{\mathbb{i}} v_{\mathbb{i}} = 1$), the reproductive values become:

$$\begin{pmatrix} v_{\mathrm{f}} & v_{\mathrm{m}} \end{pmatrix} = \begin{pmatrix} \lambda & 1-\lambda \end{pmatrix} \tag{S26}$$

And thus the reproductive values of the transitions between classes become:

$$v_{\mathrm{f}\to\mathrm{f}} = \lambda^2 \tag{S27a}$$

$$v_{\mathrm{f}\to\mathrm{m}} = \lambda(1-\lambda) \tag{S27b}$$

$$v_{\mathrm{m}\to\mathrm{f}} = (1-\lambda)\lambda \tag{S27c}$$

$$v_{\mathrm{m}\to\mathrm{m}} = (1-\lambda)^2 \tag{S27d}$$

Diploidy

Earlier, we defined $\hat{\alpha}$ to be the proportion of an individual female's transmitted breeding value that comes from her maternal-origin gene, and we defined the proportion of a individual male's transmitted breeding value that came from his paternal-origin gene to be $\hat{\beta}$. If we define the the probability that the transmitted breeding value of a female came from a female in the previous generation to be $\tilde{\alpha}$, and the probability that the transmitted breeding value of a male came from a male in the previous generation to be $\tilde{\beta}$. Then, $\tilde{\alpha} = \hat{\alpha} = \alpha$ and similarly $\tilde{\beta} = \hat{\beta} = \beta$. With this, we can write out the gene-flow matrix T as:

$$T = \begin{pmatrix} \alpha & 1-\alpha \\ 1-\beta & \beta \end{pmatrix} \tag{S28}$$

And thus the normalised class reproductive values become:

$$\begin{pmatrix} v_{\mathrm{f}} & v_{\mathrm{m}} \end{pmatrix} = \begin{pmatrix} \frac{1-\beta}{2-\alpha-\beta} & \frac{1-\alpha}{2-\alpha-\beta} \end{pmatrix} \tag{S29}$$

And the reproductive values of transitions between classes become:

$$v_{\mathrm{f}\to\mathrm{f}} = \frac{\alpha(1-\beta)}{2-\alpha-\beta} \tag{S30a}$$

$$v_{\mathrm{f}\to\mathrm{m}} = \frac{(1-\beta)(1-\alpha)}{2-\alpha-\beta} \tag{S30b}$$

$$v_{\mathrm{m}\to\mathrm{f}} = \frac{(1-\alpha)(1-\beta)}{2-\alpha-\beta} \tag{S30c}$$

$$v_{\mathrm{m}\to\mathrm{m}} = \frac{\beta(1-\alpha)}{2-\alpha-\beta} \tag{S30d}$$

6 Condition for increase

Juvenile behaviour

We first consider a locus which affects juvenile behaviour, and denote the 'transmitted' or 'genic' or 'breeding' value (Price, 1970; Falconer, 1981; Grafen, 1985) of an individual drawn at random from the population at this locus g, with g_{f} being the transmitted genic value of a randomly chosen female at this locus, and g_{m} being the transmitted genic value of a randomly chosen male. Assuming vanishing genetic variation, the condition for natural selection to favour an increase in this trait is given by:

$$\frac{\mathrm{d}W}{\mathrm{d}g} > 0 \tag{S31}$$

In a class structured population, $W = \sum_{\mathbb{i}} \sum_{\mathbb{j}} v_{\mathbb{i}\to\mathbb{j}} W_{\mathbb{i}\to\mathbb{j}}$, which is the reproductive-value weighted average of relative fitness taken across classes, with $v_{\mathbb{i}\to\mathbb{j}}$ being the reproductive value of the transition between class $\mathbb{i}$ and $\mathbb{j}$, where $\mathbb{i},\mathbb{j} \in \{\mathrm{f},\mathrm{m}\}$. Condition S31 is therefore equivalent to:

$$\sum_{\mathbb{i}} \sum_{\mathbb{j}} v_{\mathbb{i}\to\mathbb{j}} \frac{\mathrm{d}W_{\mathbb{i}\to\mathbb{j}}}{\mathrm{d}g_{\mathbb{i}}} > 0 \tag{S32}$$

In our case, we have two classes (f and m), and so can write out as:

$$v_{\mathrm{f}\to\mathrm{m}} \frac{\mathrm{d}W_{\mathrm{f}\to\mathrm{m}}}{\mathrm{d}g_{\mathrm{f}}} + v_{\mathrm{f}\to\mathrm{f}} \frac{\mathrm{d}W_{\mathrm{f}\to\mathrm{f}}}{\mathrm{d}g_{\mathrm{f}}} + v_{\mathrm{m}\to\mathrm{f}} \frac{\mathrm{d}W_{\mathrm{m}\to\mathrm{f}}}{\mathrm{d}g_{\mathrm{m}}} + v_{\mathrm{m}\to\mathrm{m}} \frac{\mathrm{d}W_{\mathrm{m}\to\mathrm{m}}}{\mathrm{d}g_{\mathrm{m}}} > 0 \tag{S33}$$

Using the chain rule, we can then expand this out to:

$$\begin{aligned}
&v_{\mathrm{f}\to\mathrm{f}} \left(\frac{\partial W_{\mathrm{f}\to\mathrm{f}}}{\partial x} \frac{\mathrm{d}x}{\mathrm{d}g_{\mathrm{f}}} + \frac{\partial W_{\mathrm{f}\to\mathrm{f}}}{\partial y_{\mathrm{f}}} \frac{\mathrm{d}y_{\mathrm{f}}}{\mathrm{d}g_{\mathrm{f}}} + \frac{\partial W_{\mathrm{f}\to\mathrm{f}}}{\partial y_{\mathrm{m}}} \frac{\mathrm{d}y_{\mathrm{m}}}{\mathrm{d}g_{\mathrm{f}}} \right) + \\
&v_{\mathrm{f}\to\mathrm{m}} \left(\frac{\partial W_{\mathrm{f}\to\mathrm{m}}}{\partial x} \frac{\mathrm{d}x}{\mathrm{d}g_{\mathrm{f}}} + \frac{\partial W_{\mathrm{f}\to\mathrm{m}}}{\partial y_{\mathrm{f}}} \frac{\mathrm{d}y_{\mathrm{f}}}{\mathrm{d}g_{\mathrm{f}}} + \frac{\partial W_{\mathrm{f}\to\mathrm{m}}}{\partial y_{\mathrm{m}}} \frac{\mathrm{d}y_{\mathrm{m}}}{\mathrm{d}g_{\mathrm{f}}} \right) + \\
&v_{\mathrm{m}\to\mathrm{f}} \left(\frac{\partial W_{\mathrm{m}\to\mathrm{f}}}{\partial x} \frac{\mathrm{d}x}{\mathrm{d}g_{\mathrm{m}}} + \frac{\partial W_{\mathrm{m}\to\mathrm{f}}}{\partial y_{\mathrm{f}}} \frac{\mathrm{d}y_{\mathrm{f}}}{\mathrm{d}g_{\mathrm{m}}} + \frac{\partial W_{\mathrm{m}\to\mathrm{f}}}{\partial y_{\mathrm{m}}} \frac{\mathrm{d}y_{\mathrm{m}}}{\mathrm{d}g_{\mathrm{m}}} \right) + \\
&v_{\mathrm{m}\to\mathrm{m}} \left(\frac{\partial W_{\mathrm{m}\to\mathrm{m}}}{\partial x} \frac{\mathrm{d}x}{\mathrm{d}g_{\mathrm{m}}} + \frac{\partial W_{\mathrm{m}\to\mathrm{m}}}{\partial y_{\mathrm{f}}} \frac{\mathrm{d}y_{\mathrm{f}}}{\mathrm{d}g_{\mathrm{m}}} + \frac{\partial W_{\mathrm{m}\to\mathrm{m}}}{\partial y_{\mathrm{m}}} \frac{\mathrm{d}y_{\mathrm{m}}}{\mathrm{d}g_{\mathrm{m}}} \right) > 0
\end{aligned} \tag{S34}$$

Substituting in our marginal fitness effects, and rewriting the derivatives as relatedness coefficients, our condition simplifies down to:

$$\begin{aligned}
&v_{\mathrm{f}} \left(-c_{\mathrm{fj}} (r^{i}_{\mathrm{ff}} - k_{\mathrm{f}} r^{p}_{\mathrm{ff}}) + (1-k_{\mathrm{f}}) (b_{\mathrm{fj}} r^{p}_{\mathrm{ff}} + b_{\mathrm{mj}} r^{p}_{\mathrm{fm}}) \right) + \\
&v_{\mathrm{m}} \left(-c_{\mathrm{mj}} (r^{i}_{\mathrm{mm}} - k_{\mathrm{m}} r^{p}_{\mathrm{mm}}) + (1-k_{\mathrm{m}}) (b_{\mathrm{fj}} r^{p}_{\mathrm{mf}} + b_{\mathrm{mj}} r^{p}_{\mathrm{mm}}) \right) > 0
\end{aligned} \tag{S35}$$

Where k_f is the scale of competition for females, and k_m is the scale of competition for males, i.e. the degree to which competition is occurring locally (Frank, 1998). We can then make some simplifications to generate the potentials for altruism seen in the main text.

Female specific behaviour

We first consider female-specific behaviour, in which case females may have marginal fitness effects upon self and others (i.e. $c_{fj} = c; b_{fj} = b$), but males have no fitness effects (i.e. $b_{mj}, c_{mj} = 0$). In which case the above equation simplifies down to:

$$-c[v_f(r^i_{ff} - k_f r^p_{ff})] + b[(1-k_f)v_f r^p_{ff} + (1-k_m)v_m r^p_{mf}] > 0 \tag{S36}$$

We can then rearrange this condition into a dimensionless potential for altruism (Gardner, 2010), where $c/b < A$. Note that this is similar to the κ of Lehmann and Rousset (2010). In this case:

$$A = \frac{(1-k_f)v_f r^p_{ff} + (1-k_m)v_m r^p_{mf}}{v_f(r^i_{ff} - k_f r^p_{ff})} \tag{S37}$$

We can then plug in the specific values for the relatedness coefficients, reproductive values, and scales of competition generated from our different inheritance systems and assumptions about demography. Under sex-symmetric dispersal ($d_f = d_m = d$, $\kappa_f = \kappa_m = (1-d)^2$) and an even sex ratio of adults breeders on each patch ($n_f = n_m = n$), then for diploidy, arrhenotoky, male PGE, and paterothylotoky, the potential for altruism simplifies down to:

$$A = \frac{1}{n} \tag{S38}$$

Which recovers the result found by Gardner (2010) in his analysis of juvenile altruism. For female maternal genome elimination:

$$A = \frac{4-(1-d)^2}{\left(4-(1-d)^2\right)n(1-\sigma) + (1-d)^2\sigma} \tag{S39}$$

Where σ represents the proportion of expression that comes from the maternal-origin gene copy in females. With this parameter we may then manipulate the degree of "control" that the maternal-origin versus paternal-origin copies have over the female phenotype. For example, if the maternal-origin gene copy exclusively determines the phenotype then $\sigma = 1$. Alternatively, if - in females - the paternal-origin copy exclusively exerts "control" over the phenotype then $\sigma = 0$.

For haploidy:

$$A = \frac{(1-\lambda)^2 + \lambda^2}{n\lambda} \tag{S40}$$

Where again, λ represents the probability that an offspring inherits their genome from their mother rather than father. When $\lambda = 1/2$, then once again $A = 1/n$.

Male specific behaviour

Similarly, for a behaviour that is male specific (i.e. $c_{fj}, b_{fj} = 0; b_{mj} = b; c_{mj} = c$):

$$A = \frac{(1-k_f)v_f r^p_{fm} + (1-k_m)v_m r^p_{mm}}{v_m(r^i_{mm} - k_m r^p_{mm})} \tag{S41}$$

We can then plug in the specific values for the relatedness coefficients and reproductive values generated from our different inheritance systems. Under sex-symmetric dispersal and an even sex ratio of adults on each patch

($d_f = d_m = d$ and $n_f = n_m = n$), then for diploidy, arrhenotoky, paterothylotoky, and female maternal-genome elimination:

$$A = \frac{1}{n} \tag{S42}$$

However, under male PGE, the potential for juvenile altruism is:

$$A = \frac{4-(1-d)^2}{\left(4-(1-d)^2\right)n(1-\tau)+(1-d)^2\tau} \tag{S43}$$

Which when $\tau = 1/2$ -i.e. when maternal-origin genes and paternal-origin genes contribute equally to the phenotype in males - recovers equation 1 of the main text. For haploidy, the potential for altruism is given by:

$$A = \frac{(1-\lambda)^2+\lambda^2}{n(1-\lambda)} \tag{S44}$$

Where again, λ represents the probability that an offspring inherits their genome from their mother rather than father.

Both sexes express the behaviour

For a behaviour expressed by both sexes (i.e. $c_{fj} = c_{mj} = c; b_{fj} = b_{mj} = b$):

$$A = \frac{(1-k_f)v_f\left(r^p_{ff}+r^p_{fm}\right)+(1-k_m)v_m\left(r^p_{mf}+r^p_{mm}\right)}{v_f\left(r^i_{ff}-k_f r^p_{ff}\right)+v_m\left(r^i_{mm}-k_m r^p_{mm}\right)} \tag{S45}$$

Once again, plugging in the values for relatedness and reproductive value under sex-neutral demography ($d_f = d_m = d$ and $n_f = n_m = n$), for diploidy, arrhenotoky, and paterothylotoky:

$$A = \frac{1}{n} \tag{S46}$$

Note that this recovers the results of Gardner (2010). Whilst there is an apparent factor of two difference between the these results this only arises because of a slight difference in how the b's are defined, otherwise they are equivalent. For male PGE:

$$A = \frac{8-2(1-d)^2}{\left(4-(1-d)^2\right)n(2-\tau)+(1-d)^2\tau} \tag{S47}$$

For female MGE:

$$A = \frac{8-2(1-d)^2}{\left(4-(1-d)^2\right)n(2-\sigma)+(1-d)^2\sigma} \tag{S48}$$

And for haploidy:

$$A = 2\frac{(1-\lambda)^2+\lambda^2}{n} \tag{S49}$$

Full expressions for arbitrary values of d_f, d_m,n_f and n_m are unwieldy. However, we plot results for the some intermediate scenarios in Figures S2-S3 and S6-S7.

Adult behaviour

We follow a similar procedure for adult specific behaviour. In which case we find the condition for a trait to increase is given by:

$$\begin{aligned} &v_f\left(-c_{fa}(r^i_{ff}-k_f r^v_{ff})+b_{fa}(r^P_{ff}-k_f r^v_{ff})+\frac{1}{\gamma}(b_{ma}-c_{ma})(r^P_{fm}-k_f r^v_{fm})\right)+ \\ &v_m\left(-c_{ma}(r^i_{mm}-k_m r^v_{mm})+b_{ma}(r^P_{mm}-k_m r^v_{mm})+\gamma(b_{fa}-c_{fa})(r^P_{mf}-k_m r^v_{mf})\right)>0 \end{aligned} \tag{S50}$$

Where $\gamma = n_f/n_m$. As before, we can rewrite this as a potential for altruism.

Female specific behaviour

First, for behaviour expressed solely by females (i.e. $c_{fa} = c; b_{fa} = b; b_{ma}, c_{ma} = 0$), the potential for altruism becomes:

$$A = \frac{v_f(r^P_{ff} - k_f r^v_{ff}) + v_m\gamma(r^P_{mf} - k_m r^v_{mf})}{v_f(r^i_{ff} - k_f r^v_{ff}) + v_m\gamma(r^P_{mf} - k_m r^v_{mf})} \tag{S51}$$

Which, when we plug in our values for the relatedness coefficients and reproductive values, then under sex-neutral demography ($d_f = d_m = d$ and $n_f = n_m = n$), the results for diploidy, arrhenotoky, paterothylotoky, and male PGE become:

$$A = \frac{1}{n} \tag{S52}$$

For female MGE:

$$A = \frac{\left(1-(1-d)^2\right)\sigma\left(4n-(n+1)(1-d)^2\right) - n\left(4-(1-d)^2\right)}{\left(n-(1-d)^2\right)\sigma\left(4n-(n+1)(1-d)^2\right) - n^2\left(4-(1-d)^2\right)} \tag{S53}$$

And for haploidy:

$$A = \frac{\lambda - (1-d)^2(1-2(1-\lambda))(1-\lambda)}{\lambda n - (1-d)^2(1-2(1-\lambda))(1-\lambda)} \tag{S54}$$

Male specific behaviour

For male specific behaviour (i.e. $c_{fa}, b_{fa} = 0; b_{ma} = b; c_{ma} = c$), the potential for altruism is:

$$A = \frac{v_m(r^P_{mm} - k_m r^v_{mm}) + v_f(1/\gamma)(r^P_{fm} - k_f r^v_{fm})}{v_m(r^i_{mm} - k_m r^v_{mm}) + v_f(1/\gamma)(r^P_{fm} - k_f r^v_{fm})} \tag{S55}$$

Which again, when we substitute in the appropriate relatedness coefficients and reproductive values, and assume sex-neutral demography ($d_f = d_m = d$ and $n_f = n_m = n$), simplify down to:

$$A = \frac{1}{n} \tag{S56}$$

For diploidy, arrhenotoky, paterothylotoky, and female MGE. Whilst for male PGE:

$$A = \frac{\left(1-(1-d)^2\right)\tau\left(4n-(n+1)(1-d)^2\right) - n\left(4-(1-d)^2\right)}{\left(n-(1-d)^2\right)\tau\left(4n-(n+1)(1-d)^2\right) - n^2\left(4-(1-d)^2\right)} \tag{S57}$$

And for haploidy:

$$A = \frac{(1-\lambda) - (1-d)^2(1-2\lambda)\lambda}{(1-\lambda)n - (1-d)^2(1-2\lambda)\lambda} \tag{S58}$$

Both sexes express the behaviour

And for behaviour expressed by both sexes (i.e. $c_{fa} = c_{ma} = c; b_{fa} = b_{ma} = b$):

$$A = \frac{v_f\left((r^P_{ff} - k_f r^v_{ff}) + (1/\gamma)(r^P_{fm} - k_f r^v_{fm})\right) + v_m\left((r^P_{mm} - k_m r^v_{mm}) + \gamma(r^P_{mf} - k_m r^v_{mf})\right)}{v_f\left((r^i_{ff} - k_f r^v_{ff}) + (1/\gamma)(r^P_{fm} - k_f r^v_{fm})\right) + v_m\left((r^i_{mm} - k_m r^v_{mm}) + \gamma(r^P_{mf} - k_m r^v_{mf})\right)} \tag{S59}$$

Once again, putting in the specific values for the relatedness coefficients and reproductive values, we find that under sex-symmetric dispersal and with an even sex-ratio of breeders then for diploidy, arrhenotoky, and paterothylotoky:

$$A = \frac{1}{n} \tag{S60}$$

For female MGE:

$$A = \frac{\left(4-(1-d)^2\right) n \left(2-\left(1-(1-d)^2\right)\sigma\right) + \left(1-(1-d)^2\right)(1-d)^2\sigma}{\left(4-(1-d)^2\right) n^2(2-\sigma) + \left(5-(1-d)^2\right)(1-d)^2 n\sigma - (1-d)^4\sigma} \tag{S61}$$

For male PGE:

$$A = \frac{\left(4-(1-d)^2\right) n \left(2-\left(1-(1-d)^2\right)\tau\right) + \left(1-(1-d)^2\right)(1-d)^2\tau}{\left(4-(1-d)^2\right) n^2(2-\tau) + \left(5-(1-d)^2\right)(1-d)^2 n\tau - (1-d)^4\tau} \tag{S62}$$

And for haploidy:

$$A = \frac{1+(1-d)^2(1-2\lambda)^2}{n+(1-d)^2(1-2\lambda)^2} \tag{S63}$$

Once again, full expressions for the sex-biased scenarios are cumbersome to present, but instead we plot some of these scenarios in Figures S4-S5 and S8-S9.

7 Figures

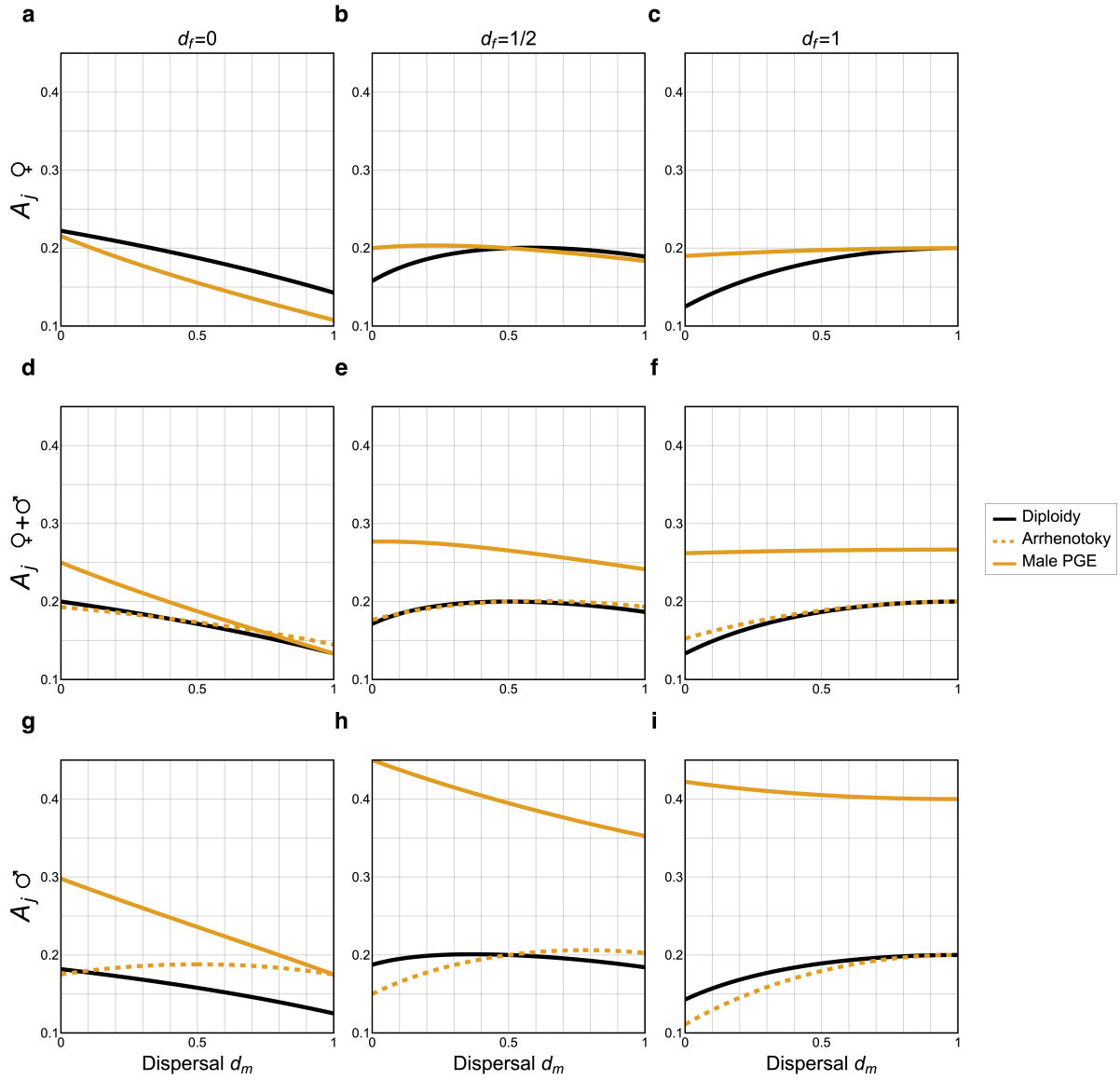

Figure S2: **The potential for altruism amongst juveniles A_j when there are sex-biases in dispersal**. In all panels $n_f = n_m = 5$ and $d_m = 1/2$. For the case of male PGE we assume $\tau = 1/2$. Methods to regenerate these plots can be found in SM§1-6.

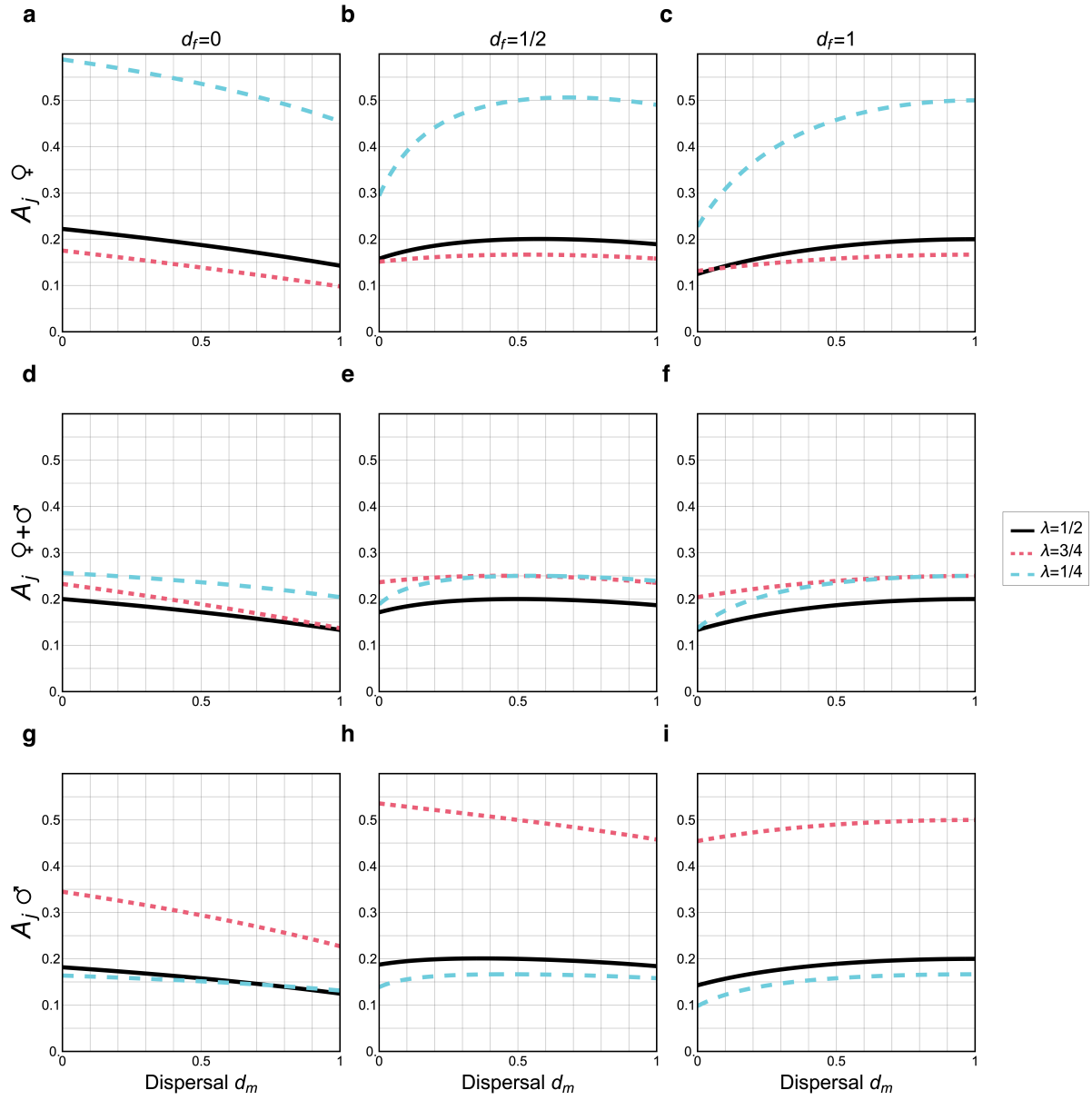

Figure S3: **The potential for altruism amongst haploid juveniles A_j when there are sex-biases in dispersal, and varying extents of sex-biased transmission λ.** In all panels $n_f = n_m = 5$ and $d_m = 1/2$. Methods to regenerate these plots can be found in SM§1-6.

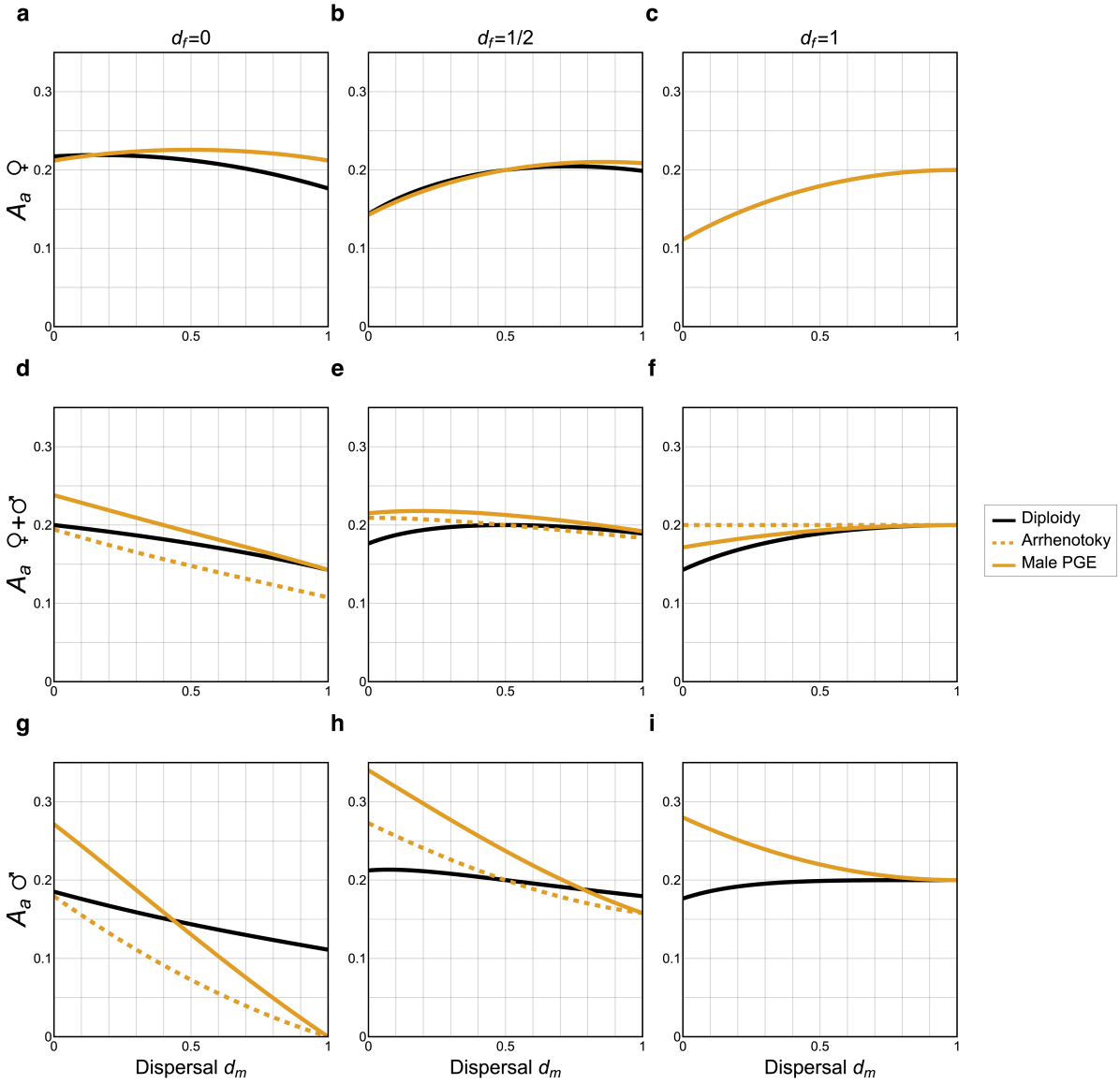

Figure S4: **The potential for altruism amongst adults A_a when there are sex-biases in dispersal**. In all panels $n_f = n_m = 5$ and $d_m = 1/2$. For the case of male PGE we assume $\tau = 1/2$. Methods to regenerate these plots can be found in SM§1-6.

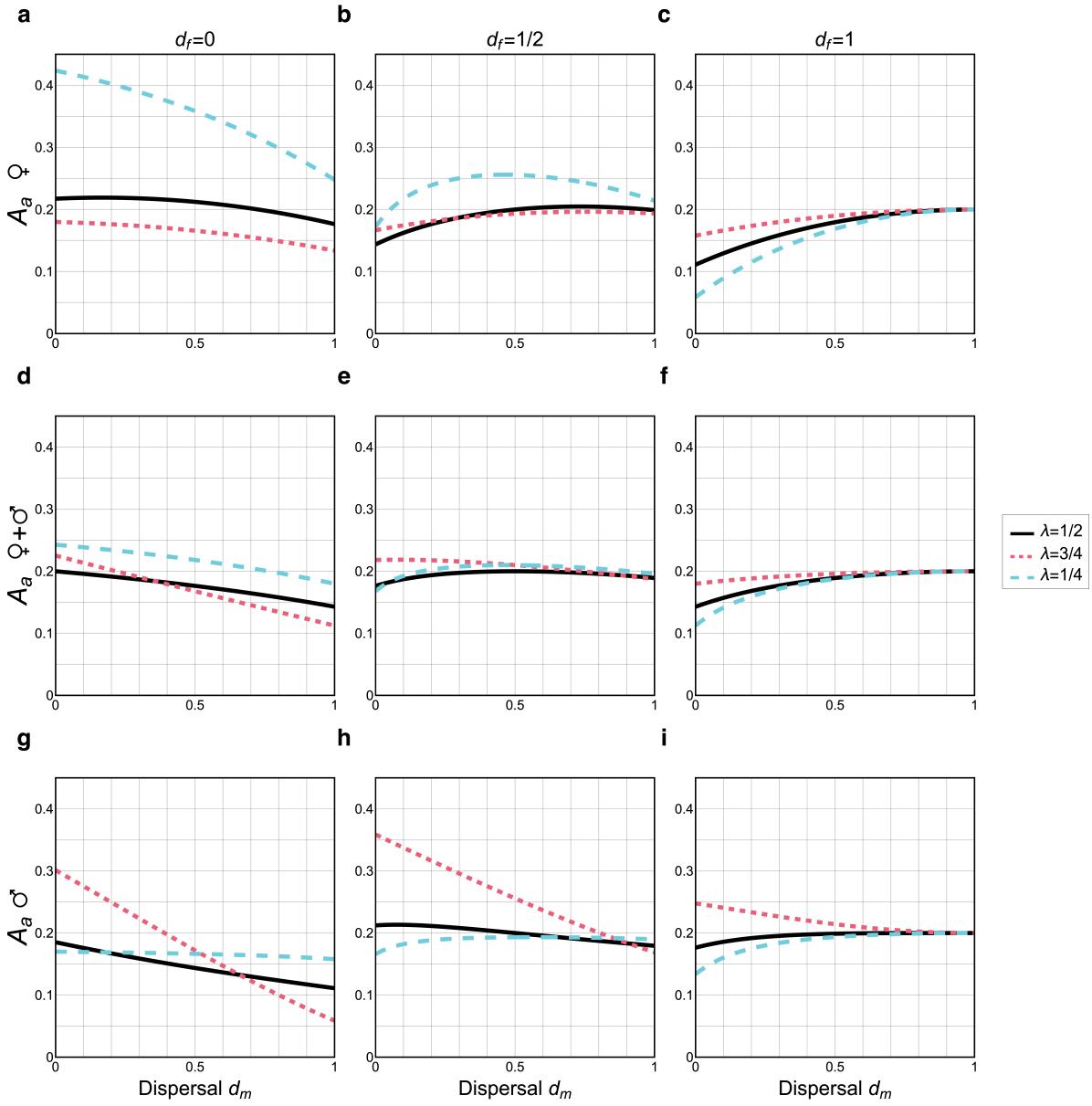

Figure S5: **The potential for altruism amongst haploid adults A_a when there are sex-biases in dispersal, and varying extents of sex-biased transmission λ.** In all panels $n_f = n_m = 5$ and $d_m = 1/2$. Methods to regenerate these plots can be found in SM§1-6.

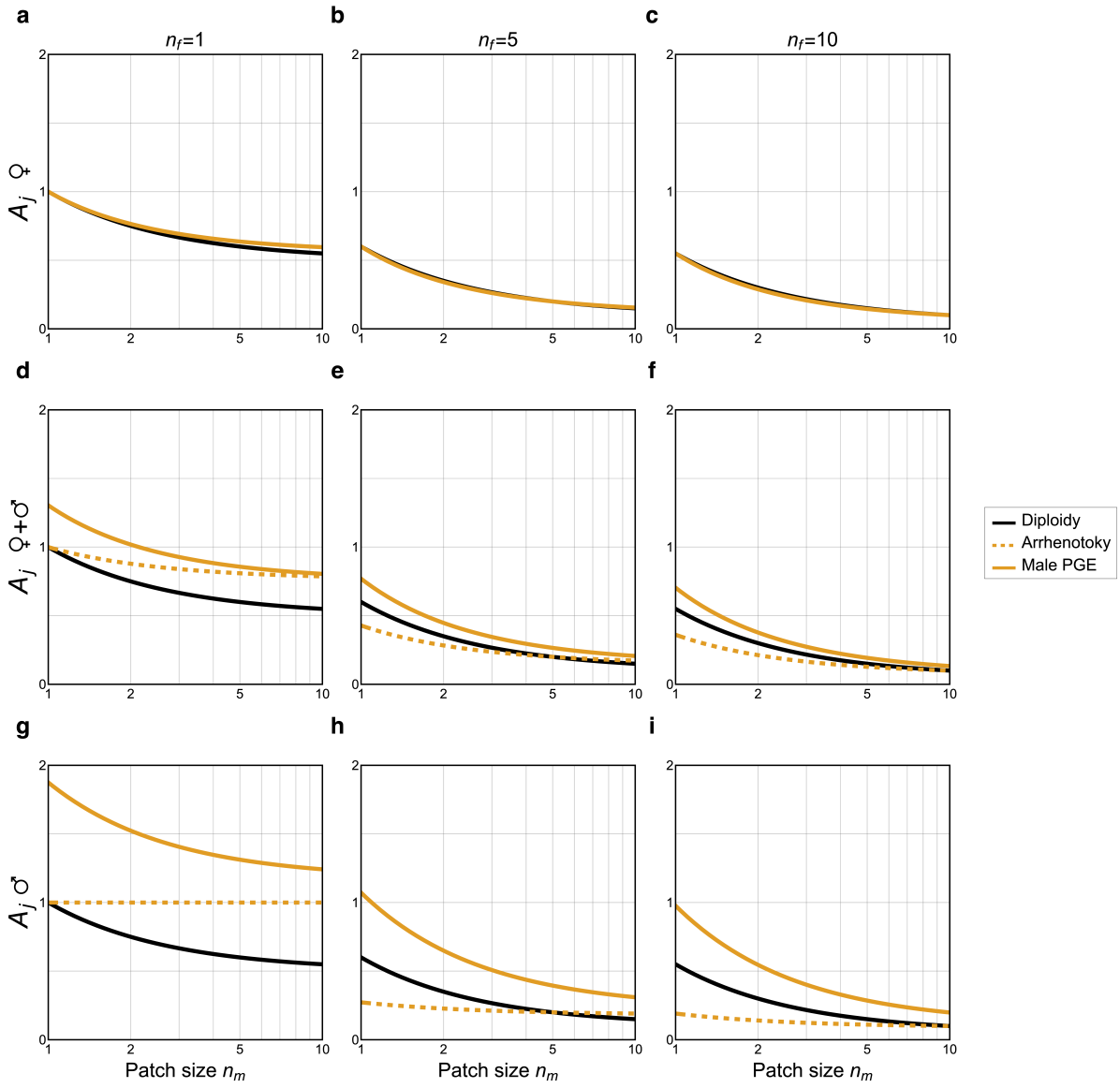

Figure S6: **The potential for altruism amongst juveniles A_j when there are sex-biases in the number of adult breeders per patch**. In all panels $d_\mathrm{f} = d_\mathrm{m} = 1/2$ and $n_\mathrm{m} = 5$. For the case of male PGE we assume $\tau = 1/2$. Methods to regenerate these plots can be found in SM§1-6.

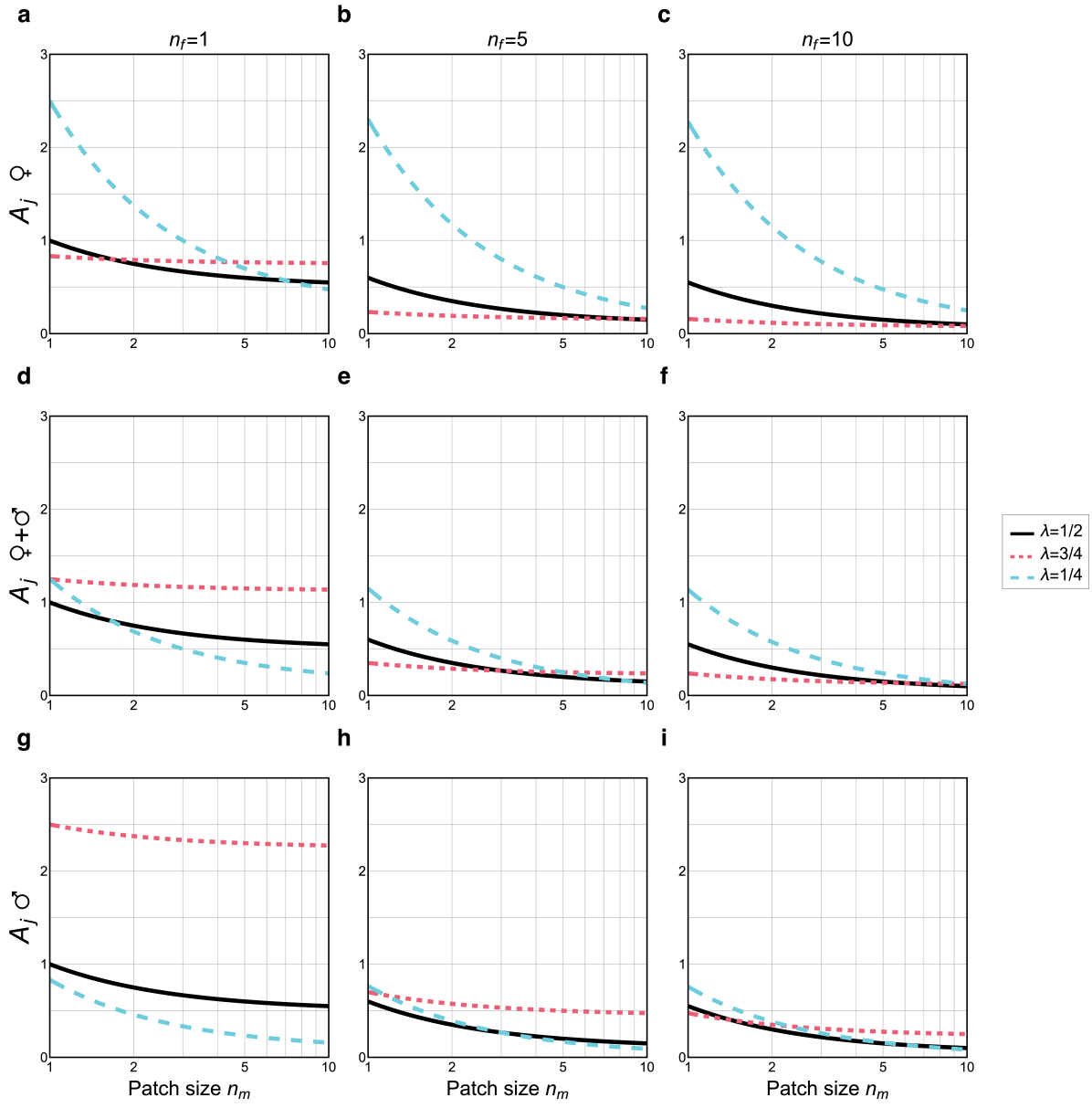

Figure S7: **The potential for altruism amongst haploid juveniles A_j when there are sex-biases in the number of adult breeders per patch, and varying extents of sex-biased transmission λ.** In all panels $d_f = d_m = 1/2$ and $n_m = 5$. Methods to regenerate these plots can be found in SM§1-6.

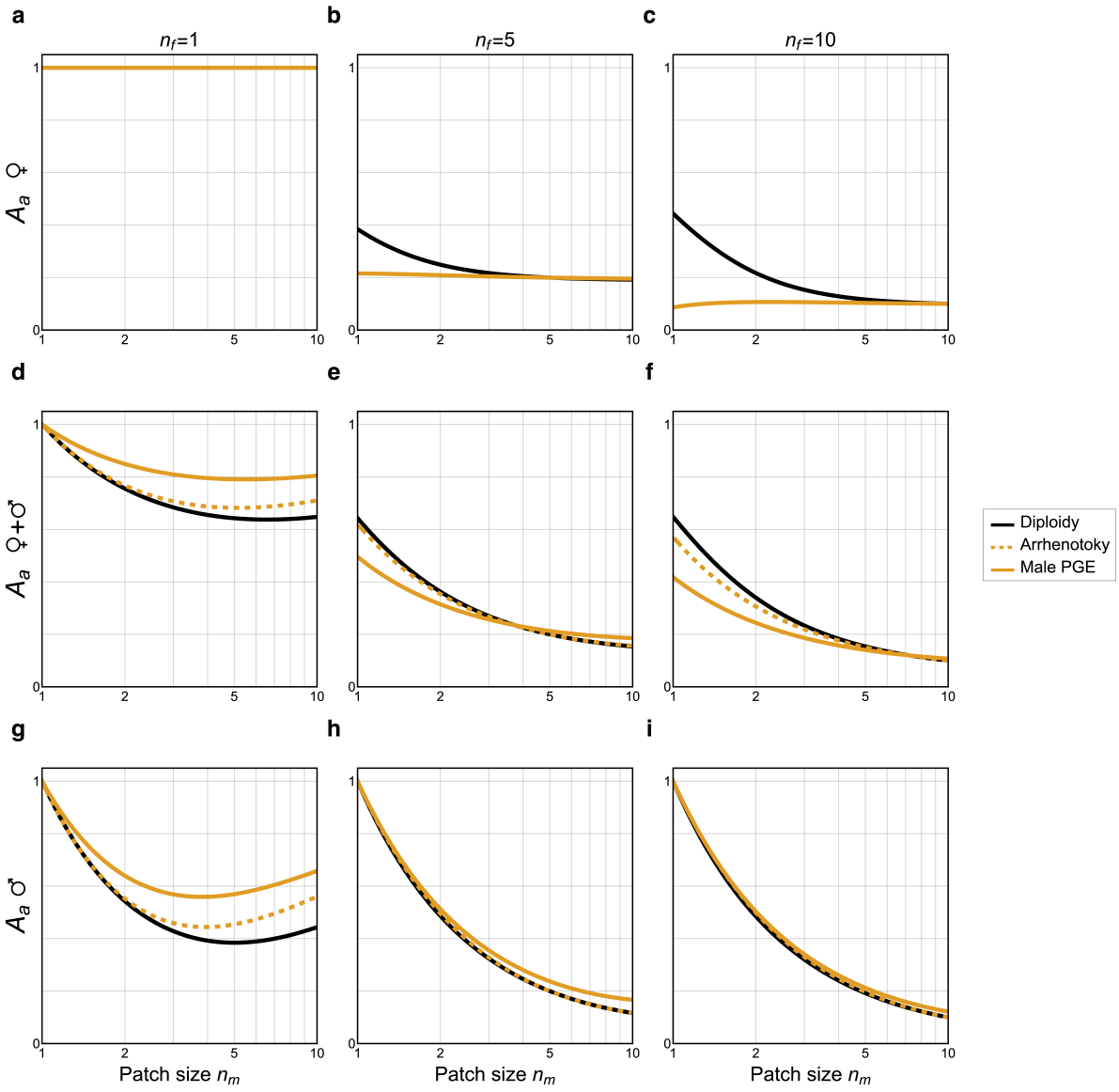

Figure S8: **The potential for altruism amongst adults A_a when there are sex-biases in the number of adult breeders per patch**. In all panels $d_f = d_m = 1/2$ and $n_m = 5$. For the case of male PGE we assume $\tau = 1/2$. Methods to regenerate these plots can be found in SM§1-6.

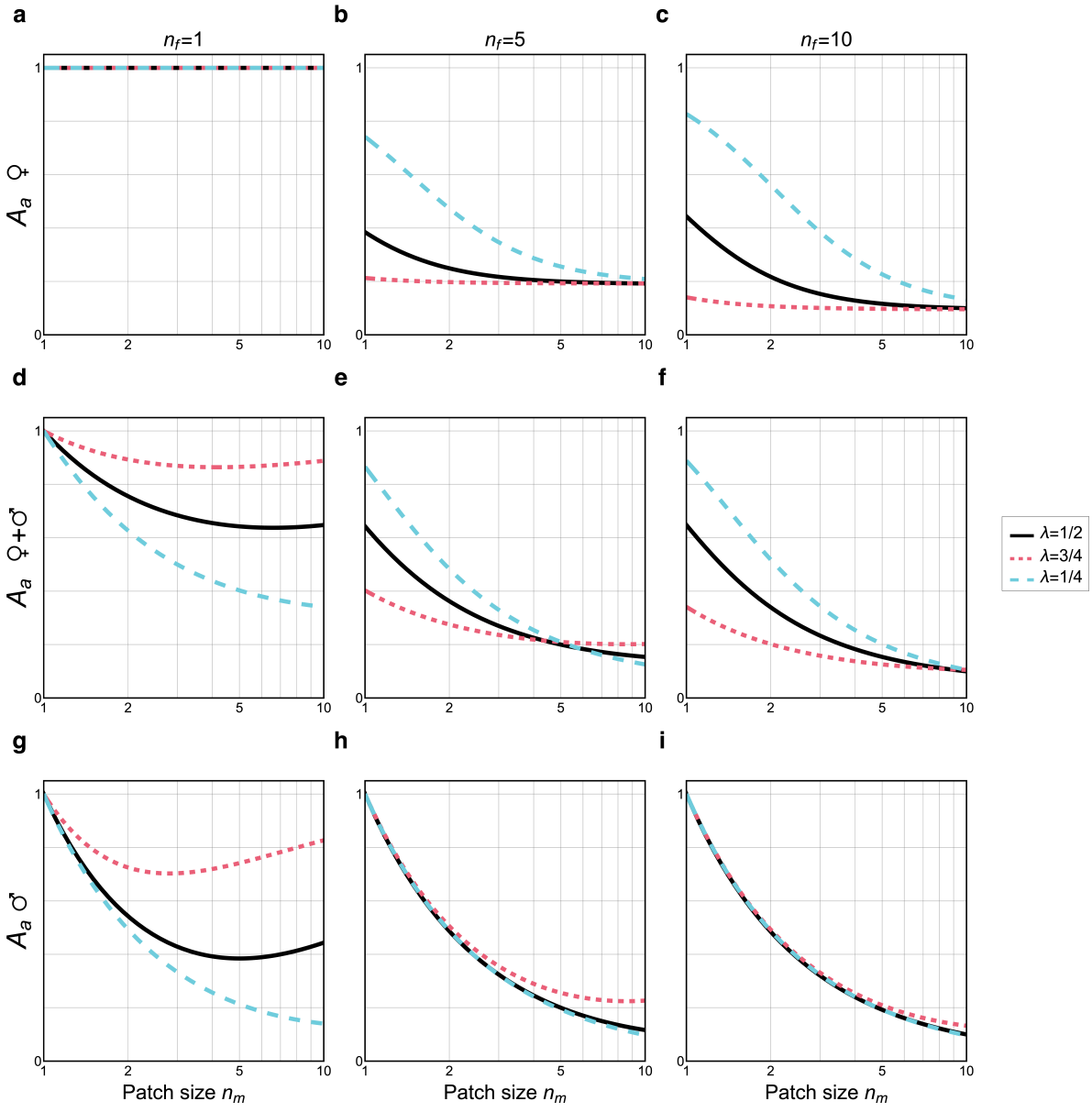

Figure S9: **The potential for altruism amongst haploid adults A_a when there are sex-biases in the number of adult breeders per patch, and varying extents of sex-biased transmission λ.** In all panels $d_f = d_m = 1/2$ and $n_m = 5$. Methods to regenerate these plots can be found in SM§1-6.

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