

# A population ecology approach

Mark Schaffer, Paul Seabright

November 4, 2010

## 1 Basic setup

Our basic aim is to explain how the competition between two alleles can be influenced by the relative propensity for the bearer to be selected as a mate in preference to the bearer of a rival allele. The selection effect on equilibrium allele frequencies may outweigh the impact of allele's intrinsic effect on fecundity.

What interests us in this model is that the strength of the sexual selection component is itself the outcome of natural selection. In other words, we suppose that mate preferences are themselves determined by alleles subject to selection.

We extend this idea to explain the selection of alleles favouring cooperation within groups due to evolution of a preference on the part of the groups for members displaying cooperative behaviour. This extends, in effect, the mechanism of sexual selection beyond the pairwise mating structure standard in this literature.

We start with a simple model that illustrates the coevolution of the allele determining selection and the allele determining behaviour. We call the two forms of behaviour "cooperation" and "selfishness" in anticipation of the later extension. For now, "cooperation" means simply greater fecundity than "selfish" behaviour. We could perhaps at this stage label these "green" and "red". "Green" can but does not necessarily have to have a higher payoff (fecundity) than red. We show that even if "green" has higher fecundity, depending on other parameters equilibria may exist where "green" is driven to zero frequency.

Upper case Roman letters indicate numbers of individuals. Lower case indicate proportions. Genes are indicated with Greek letters. Alleles are indicated with Roman letters.

Consider the simplest sexual selection version, with 1 adult male and 1 adult female, and discrete strategy spaces.

$\theta$  is the cooperation gene, expressed by the female.  $\theta \in [A, a]$ , where  $A$  means "cooperate" ("altruist") and  $a$  means "selfish".

$\Gamma$  is the gatekeeper gene, expressed by the adult male.  $\Gamma \in [G, g]$ . A male carrying  $G$  prefers to adopt a female carrying  $A$ , and similarly for  $g$  and  $a$ .

This gives us 4 genotypes for each sex:  $GA$ ,  $Ga$ ,  $gA$ , and  $ga$ .

There are two phenotypes for males: "prefer  $A$ ", expressed by  $GA$  and  $Ga$  males, and "prefer  $a$ ", expressed by  $gA$  and  $ga$  males.

There are two phenotypes for females: "cooperate", expressed by  $GA$  and  $gA$  females, and "be selfish", expressed by  $Ga$  and  $ga$  females.

The adult male population is normalized to 1, so we are assuming a fixed carrying capacity for the environment.

The females engage in foraging activity that generates resources. Mating results in offspring, and the greater the resources from foraging the greater the number of offspring. After the offspring are born, the female children are expelled to find new groups to join (exogamy), and the male children stay behind.

In this simple version, foraging yields total payoffs  $\Pi_i = \Pi(\theta_i)$ , total fecundity is  $2\Pi_i$  (we multiply by 2 so we don't have split between male and female children), and we assume  $\Pi_A > \Pi_a$ , so "cooperation" always generates more resources than selfish behaviour. ("Cooperation" is a misnomer here. We introduce it later when we move to a multi-female model.)

Another simplification in this simple version, there is only one male "slot" available, and we assume that which of the male children gets this slot and grows to adulthood is randomly selected. There is only one female "slot" available, and the female is selected from the total adoption pool by this adult male. Which type of female is selected depends on the male genotype, the female genotype, the numbers of different types of females from which to choose, and how readily a male can distinguish between the two phenotypes of females.

$m_{\Gamma\theta}$  is the share (or number, since the population=1) of the adult population carrying alleles  $\Gamma$ . and  $\theta$ . Since survival to adulthood is random in the above sense, these are also the proportions of male children. The 4 genotypes of adult males sum to one (of course):

$$m_{GA} + m_{Ga} + m_{gA} + m_{ga} = 1.$$

It is notationally more convenient to work with shares of female children in the adoption pool:

$$f_{GA} + f_{Ga} + f_{gA} + f_{ga} = 1$$

In fact, since the sex ratio is assumed to be one,  $m_{\Gamma\theta} \equiv f_{\Gamma\theta}$ , i.e., the frequency of the male child genotype equals the frequency of the male adult genotype (by the assumption of random

male survival) equals the frequency of the female child genotype in the adoption pool. But because survival to adulthood and mating is different for males and females, we will still need to distinguish between frequencies of male and female genotypes.

It is sometimes convenient to work with population shares by phenotype. These are

$$m_G \equiv m_{GA} + m_{Ga}$$

$$m_g \equiv 1 - m_G$$

$$f_A \equiv f_{GA} + f_{gA}$$

$$f_a \equiv 1 - f_A$$

We assume that there are more female children available  $N$  than there are slots for them to fill (1). The corresponding numbers of female children in the adoption pool are:

$$Nf_{GA} + Nf_{Ga} + Nf_{gA} + Nf_{ga} = N$$

## 2 Mate selection, a.k.a. "adoption"

In this section we discuss how females are matched to males. We refer to this variously as mate selection, matching, or adoption.

This is a model of exogamy, and females are the ones who expel and then chosen, or not, by males to join them as mates.  $G$ -males prefer to choose  $A$ -females, and  $g$ -men prefer  $a$ -women. The type of female is not perfectly observable by males, so except in special cases we will get imperfect matching.

We abuse economic terminology a bit and refer to "signalling" by females and "screening" by males. "Signalling" means the female takes an action that signals her type. In our model, females signal by going into one of two adoption pools,  $A$  or  $a$ . "Screening" means a male inspects the females and tries to decide which are his type and which are not. In our model, males inspect the females of a particular pool, and try to exclude females who are not their type. We can think of this as taking place in a two-step procedure; first female signalling, then male screening and mate selection.

The discrimination parameter that captures female signalling is  $d = [0.5, 1]$ . The intuitive interpretation is that it is the probability that a female of type  $\theta$  chooses to join the  $\theta$  adoption pool.  $d = 1$  means a  $\theta$  female always chooses the  $\theta$  adoption pool.  $d = 0.5$  means a  $\theta$  female chooses randomly between the two adoption pools. We allow signalling to vary between female phenotypes, i.e.,  $d_A = [0.5, 1]$  and  $d_a = [0.5, 1]$ . Thus if  $d_A = d_a = 1$ , after the signalling

stage the  $A$  pool is 100%  $A$ -females, and the  $a$  pool is 100%  $a$ -females. On the other hand, if  $d_A = d_a = 0.5$ , then after the signalling stage the  $A$  pool and  $a$  pools have compositions that are identical to each other and to the total adoption, i.e.,  $f_A$  and  $f_a \equiv 1 - f_A$ .

The discrimination parameter that captures male screening is  $e = [0, 1]$ . The intuitive interpretation is males inspect the members of the appropriate adoption pool, and try to exclude females that are not of their type. We assume that males cannot mistakenly exclude females that *are* of their type; the only mistakes they can make are not to exclude females that are not of their type. In statistical language, the null is that the candidate female is suitable, and men get to ask questions that enable them sometimes to correctly reject the null. Only Type II errors possible (don't reject the null even though it's wrong); no Type I errors possible (incorrect rejection of null). If  $e = 1$ , males can correctly identify unsuitable females 100% of the time. If  $e = 0$ , males are hopelessly indecisive, and cannot exclude any unsuitable females from the adoption pool. We allow the discriminatory powers of males to vary between male phenotypes, i.e.,  $e_A = [0, 1]$  and  $e_a = [0, 1]$ .

To summarize, the mate selection scheme we have is equivalent to two enormous versions of the "Dating Game" ("Blind Date"):

1. Signalling: Ask all the female children in the adoption population one question: "Are you an  $A$  type or an  $a$  type?" Females who answer  $A$  go into the  $A$  pool, and females answer  $a$  go into the  $a$  pool. Some females mistakenly go into the "wrong" pool; the  $A$  pool will have some  $a$  females in it, and the  $a$  pool will have some  $A$  females in it.
2. Screening:  $G$  males now inspect the female members of the  $A$  pool, and ask questions of the females that enable them to identify and exclude some  $a$  females.  $g$ -men inspect the females of the  $a$  pool, and ask questions that enable them to identify and exclude some  $A$ -women.
3. Mate selection:  $G$  males choose mates randomly from the remaining members of the  $A$  pool, and  $g$  men choose mates randomly from the remaining members of the  $a$  pool.

We ignore the problem that there may be more men than remaining female members of the corresponding pool ("depletion"). This can be addressed in an ad hoc way, e.g., topping up one adoption pool with females from the other pool. (This constraint in any case virtually never arises in practice in the simulations.)

The structure of mating as a single giant dating game is at first somewhat unappealing, but one way to justify it is as a discrete time version of a more appealing continuous time model. In the continuous time version, we would have a steady flow of infinitesimally-sized dating games.

Denote by  $S(\Gamma, \theta)$  the probability that a male of genotype  $\Gamma$  obtains a mate of genotype  $\theta$ . Thus  $S(G, A)$  is the probability that a male of type  $G$  gets a mate with his preferred feature  $A$ .

Ignoring the depletion problem in (6), we have

$$S(G, A) = \frac{d_A f_A}{d_A f_A + (1 - e_A)(1 - d_a) f_a}$$

$$S(G, a) = 1 - S(G, A)$$

$$S(g, a) = \frac{d_a f_a}{d_a f_a + (1 - e_a)(1 - d_A) f_A}$$

$$S(g, A) = 1 - S(g, a)$$

An important feature of the matching structure above is that imperfect signalling - but *not* imperfect screening - has a negative externality. Thus as  $d_A$  falls, so does  $S(G, A)$ , the probability of a  $G$ -man finding an  $A$ -woman as a mate. But  $S(g, a)$ , the probability of a  $g$ -man finding an  $a$ -woman *also* falls ( $d_A$  appears in the denominator). What happens is that when  $a$ -women make signalling mistakes, they make it harder for  $A$ -men to find them (they are joining the wrong pool), but they also make it harder for  $g$ -men to find  $a$ -women (by "polluting" the  $a$  pool). This externality does not appear with imperfect screening; a decrease in  $e_A$  makes it harder for a  $G$ -man to find an  $A$ -woman, but has no impact on the probability that a  $g$ -man finds an  $a$ -woman.

This externality turns out to be important for the ability of genes to invade. For example, say  $a$  is dominant in the population. Signalling mistakes by  $a$ -women have only a small negative impact on  $S(g, a)$ . But they have a *large* negative impact on  $S(G, A)$ , i.e., they make it considerably harder for  $G$ -men to find the few available  $A$ -women. In the simulations, an increase in  $d_a$ , i.e., improved signalling by  $a$  females, typically makes it *easier* for  $A$ -women and  $G$ -men to invade.

For the special case of random signalling,  $d_A = d_a = 0.5$  and female signals have no information content, we have

$$S(G, A) = \frac{f_A}{f_A + (1 - e_A) f_a}$$

$$S(G, a) = 1 - S(G, A)$$

$$S(g, a) = \frac{f_a}{f_a + (1 - e_a) f_A}$$

$$S(g, A) = 1 - S(g, a)$$

For the special case of random screening,  $e_A = e_a = 0$ , we have

$$S(G, A) = \frac{d_A f_A}{d_A f_A + (1 - d_a) f_a}$$

$$S(G, a) = 1 - S(G, A)$$

$$S(g, a) = \frac{d_a f_a}{d_a f_a + (1 - d_A) f_A}$$

$$S(g, A) = 1 - S(g, a)$$

After adoption, the female children become the next generation's adult females, go foraging, have offspring, etc. Unadopted female children die.

### 3 Dynamics: 1 Male, 1 Female

We have 16 possible types of pairings of males and females carrying genes  $\Gamma$  and  $\theta$ :  $GA$  (male) adopts and mates with  $GA$  (female),  $GA$  (male) adopts and mates with  $Ga$  (female), etc. Children inherit their  $\Gamma$  gene with equal probability from the father or mother, and similarly for the  $\theta$  gene.

When the female is phenotype  $A$ , the number of offspring will be  $2\Pi_A$ , and when the female is phenotype  $a$  the number of offspring will be  $2\Pi_a$ .

We can now write out the recurrence relations for the model. We begin by writing out  $m$  for male ratios and  $f$  for female (adoption pool, child) ratios. As noted above, the frequencies for male genotypes are the same for male children and male adults, by virtual of the assumption of random male survival.

Male and female recurrence relations differ in the following way. Each "family" has a single surviving male child that grows to adulthood who is randomly chosen from all the male children. (We assume away the problem that a family could "disappear" because the mother happens to have no male children.) This means that the fecundity of the mother is irrelevant. The probability that the surviving male child will be drawn from one of the possible 4 genotypes depends only on the distribution of these genotypes among the mother's children, and not on the total number of children she produces.

By contrast, female fecundity matters because of the "dating game" structure of adoption. Females of phenotype  $A$  will send more female children into the adoption pool, and therefore, *ceteris paribus*, will be more likely to have female children that are adopted. The *ceteris paribus* qualification is important, of course, because adoption also depends on the distribution of the  $G$  and  $g$  phenotypes among the adult males doing the adopting.

The male recurrence relations are:

$$m'_{GA} =$$

$$\begin{aligned}
& m_{GA}S(G, A) \frac{f_{GA} + \frac{1}{2}f_{gA}}{f_A} \\
& + \\
& m_{GA}S(G, a) \frac{\frac{1}{2}f_{Ga} + \frac{1}{4}f_{ga}}{f_a} \\
& + \\
& m_{Ga}S(G, A) \frac{\frac{1}{2}f_{GA} + \frac{1}{4}f_{gA}}{f_A} \\
& + \\
& m_{Ga}S(G, a)\{0\} \\
& + \\
& m_{gA}S(g, A) \frac{\frac{1}{2}f_{GA}}{f_A} \\
& + \\
& m_{gA}S(g, a) \frac{\frac{1}{4}f_{Ga}}{f_a} \\
& + \\
& m_{ga}S(g, A) \frac{\frac{1}{4}f_{GA}}{f_A} \\
& + \\
& m_{ga}S(g, a)\{0\}
\end{aligned}$$

$$\begin{aligned}
m'_{Ga} = & \\
& m_{GA}S(G, A)\{0\} \\
& + \\
& m_{GA}S(G, a) \frac{\frac{1}{2}f_{Ga} + \frac{1}{4}f_{ga}}{f_a} \\
& + \\
& m_{Ga}S(G, A) \frac{\frac{1}{2}f_{GA} + \frac{1}{4}f_{gA}}{f_A} \\
& + \\
& m_{Ga}S(G, a) \frac{f_{Ga} + \frac{1}{2}f_{ga}}{f_a} \\
& + \\
& m_{gA}S(g, A)\{0\} \\
& + \\
& m_{gA}S(g, a) \frac{\frac{1}{4}f_{Ga}}{f_a} \\
& + \\
& m_{ga}S(g, A) \frac{\frac{1}{4}f_{GA}}{f_A} \\
& + \\
& m_{ga}S(g, a) \frac{\frac{1}{2}f_{Ga}}{f_a}
\end{aligned}$$

$$\begin{aligned}
m'_{gA} = & \\
& m_{GA}S(G, A) \frac{\frac{1}{2}f_{gA}}{f_A} \\
& + \\
& m_{GA}S(G, a) \frac{\frac{1}{4}f_{ga}}{f_a}
\end{aligned}$$

$$\begin{aligned}
& + \\
& m_{Ga}S(G, A)\frac{\frac{1}{4}f_{gA}}{f_A} \\
& + \\
& m_{Ga}S(G, a)\{0\} \\
& + \\
& m_{gA}S(g, A)\frac{\frac{1}{2}f_{GA} + f_{gA}}{f_A} \\
& + \\
& m_{gA}S(g, a)\frac{\frac{1}{4}f_{Ga} + \frac{1}{2}f_{ga}}{f_a} \\
& + \\
& m_{ga}S(g, A)\frac{\frac{1}{4}f_{GA} + \frac{1}{2}f_{gA}}{f_A} \\
& + \\
& m_{ga}S(g, a)\{0\} \\
\\
m'_{ga} = & \\
& m_{GA}S(G, A)\{0\} \\
& + \\
& m_{GA}S(G, a)\frac{\frac{1}{4}f_{ga}}{f_a} \\
& + \\
& m_{Ga}S(G, A)\frac{\frac{1}{4}f_{gA}}{f_A} \\
& + \\
& m_{Ga}S(G, a)\frac{\frac{1}{2}f_{ga}}{f_a} \\
& + \\
& m_{gA}S(g, A)\{0\} \\
& + \\
& m_{gA}S(g, a)\frac{\frac{1}{4}f_{Ga} + \frac{1}{2}f_{ga}}{f_a} \\
& + \\
& m_{ga}S(g, A)\frac{\frac{1}{4}f_{GA} + \frac{1}{2}f_{gA}}{f_A} \\
& + \\
& m_{ga}S(g, a)\frac{\frac{1}{2}f_{Ga} + f_{ga}}{f_a}
\end{aligned}$$

Each line is the contribution of male genotype (first term), a probability that the male has a particular type of mate (second term), and the shares of the female phenotype ( $A$  or  $a$ ) weighted by the expected number of offspring contributing to the male genotype in question.

For example, in the first term for the recurrence relation for  $m'_{GA}$ , the denominator of the fraction is the frequency of the female phenotype  $A$ , i.e.,  $f_A \equiv f_{GA} + f_{gA}$ . The numerator is the contributions of the two female genotypes,  $f_{GA} + \frac{1}{2}f_{gA}$ . The reason  $f_{GA}$  gets a weight of 1 and  $f_{gA}$  gets a weight of  $\frac{1}{2}$  is because all the male children of the male-female  $GA - GA$  pairing will be  $GA$ , whereas only half of the children of the male-female pairing  $GA - gA$  will be  $GA$ .



The zeros in  $\{\}$  arise because it is impossible for a pairing of, e.g., a  $Ga$  father and a  $Ga$  mother to have a  $GA$  child.

The female recurrence relations are similar, but each term is weighted by the relative fecundity of the mother. Relative fecundity is number of female children produced  $\Pi_i$  normalized by  $N'$ , the total number of female children in the next generation, i.e., all potential female adoptees.  $N'$  is

$$N' \equiv \{m_G S(G, A) + m_g S(g, A)\} \Pi_A + \{m_G S(G, a) + m_g S(g, a)\} \Pi_a$$

The terms in the two sets of  $\{\}$  are the total numbers of female adoptees of the two phenotypes  $A$  and  $a$ , multiplied by their respective absolute fecundity  $\Pi_i$ . (Recall that a female's total fecundity is  $2\Pi_i$ , split equally between male and female children.)

The female recurrence relations are:

$$\begin{aligned} f'_{GA} = & m_{GA} S(G, A) \frac{f_{GA} + \frac{1}{2} f_{gA}}{f_A} \frac{\Pi_A}{N'} \\ & + m_{GA} S(G, a) \frac{\frac{1}{2} f_{Ga} + \frac{1}{4} f_{ga}}{f_a} \frac{\Pi_a}{N'} \\ & + m_{Ga} S(G, A) \frac{\frac{1}{2} f_{GA} + \frac{1}{4} f_{gA}}{f_A} \frac{\Pi_A}{N'} \\ & + m_{Ga} S(G, a) \{0\} \\ & + m_{gA} S(g, A) \frac{\frac{1}{2} f_{GA}}{f_A} \frac{\Pi_A}{N'} \\ & + m_{gA} S(g, a) \frac{\frac{1}{4} f_{Ga}}{f_a} \frac{\Pi_a}{N} \\ & + m_{ga} S(g, A) \frac{\frac{1}{4} f_{GA}}{f_A} \frac{\Pi_A}{N'} \\ & + m_{ga} S(g, a) \{0\} \end{aligned}$$

$$\begin{aligned} f'_{Ga} = & m_{GA} S(G, A) \{0\} \\ & + m_{GA} S(G, a) \frac{\frac{1}{2} f_{Ga} + \frac{1}{4} f_{ga}}{f_a} \frac{\Pi_a}{N'} \\ & + m_{Ga} S(G, A) \frac{\frac{1}{2} f_{GA} + \frac{1}{4} f_{gA}}{f_A} \frac{\Pi_A}{N'} \\ & + \end{aligned}$$

$$\begin{aligned}
& m_{Ga}S(G, a) \frac{f_{Ga} + \frac{1}{2}f_{ga}}{f_a} \frac{\Pi_a}{N'} \\
& + \\
& m_{gA}S(g, A)\{0\} \\
& + \\
& m_{gA}S(g, a) \frac{\frac{1}{4}f_{Ga}}{f_a} \frac{\Pi_a}{N'} \\
& + \\
& m_{ga}S(g, A) \frac{\frac{1}{4}f_{GA}}{f_A} \frac{\Pi_A}{N'} \\
& + \\
& m_{ga}S(g, a) \frac{\frac{1}{2}f_{Ga}}{f_a} \frac{\Pi_a}{N'}
\end{aligned}$$

$$f'_{gA} =$$

$$\begin{aligned}
& m_{GA}S(G, A) \frac{\frac{1}{2}f_{gA}}{f_A} \frac{\Pi_A}{N'} \\
& + \\
& m_{GA}S(G, a) \frac{\frac{1}{4}f_{ga}}{f_a} \frac{\Pi_a}{N'} \\
& + \\
& m_{Ga}S(G, A) \frac{\frac{1}{4}f_{gA}}{f_A} \frac{\Pi_A}{N'} \\
& + \\
& m_{Ga}S(G, a)\{0\} \\
& + \\
& m_{gA}S(g, A) \frac{\frac{1}{2}f_{GA} + f_{gA}}{f_A} \frac{\Pi_A}{N'} \\
& + \\
& m_{gA}S(g, a) \frac{\frac{1}{4}f_{Ga} + \frac{1}{2}f_{ga}}{f_a} \frac{\Pi_a}{N'} \\
& + \\
& m_{ga}S(g, A) \frac{\frac{1}{4}f_{GA} + \frac{1}{2}f_{gA}}{f_A} \frac{\Pi_A}{N'} \\
& + \\
& m_{ga}S(g, a)\{0\}
\end{aligned}$$

$$f'_{ga} =$$

$$\begin{aligned}
& m_{GA}S(G, A)\{0\} \\
& + \\
& m_{GA}S(G, a) \frac{\frac{1}{4}f_{ga}}{f_a} \frac{\Pi_a}{N'} \\
& + \\
& m_{Ga}S(G, A) \frac{\frac{1}{4}f_{gA}}{f_A} \frac{\Pi_A}{N'} \\
& + \\
& m_{Ga}S(G, a) \frac{\frac{1}{2}f_{ga}}{f_a} \frac{\Pi_a}{N'} \\
& + \\
& m_{gA}S(g, A)\{0\} \\
& +
\end{aligned}$$

$$\begin{aligned}
& m_{gA}S(g, a) \frac{\frac{1}{4}f_{Ga} + \frac{1}{2}f_{ga}}{f_a} \frac{\Pi_a}{N'} \\
& + \\
& m_{ga}S(g, A) \frac{\frac{1}{4}f_{GA} + \frac{1}{2}f_{gA}}{f_A} \frac{\Pi_A}{N'} \\
& + \\
& m_{ga}S(g, a) \frac{\frac{1}{2}f_{Ga} + f_{ga}}{f_a} \frac{\Pi_a}{N'}
\end{aligned}$$

## 4 Cooperation and exogamy

The structure of the simple model above is a standard-ish sexual selection model with differential fertility. In this section we expand the model to the case of cooperation.

The male side of the model is unchanged from above: each male occupies a single niche that belongs to his family. One male child is randomly selected to be the adult male in the next generation.

Each male adopts two female mates. As above, a  $G$  male preferentially selects  $A$  females as mates, and similarly for  $g$  males and  $a$  female mates.

After two females are adopted, they forage together. Female payoffs depend on their own strategy  $\theta_i$  and on the strategy of the other female  $\theta_{-i}$ . These payoffs have a prisoner's dilemma structure.

$$\Pi(a, A) > \Pi(A, A) > \Pi(a, a) > \Pi(A, a)$$

where the first argument indicates the behaviour of the first player (player  $i$ ) and the second argument indicates the behaviour of her opponent ( $-i$ ).

We can write this more compactly with subscripts:

$$\Pi_{aA} > \Pi_{AA} > \Pi_{aa} > \Pi_{Aa}$$

The male recurrence relations are:

$$\begin{aligned}
m'_{GA} = & \\
& m_{GA}S(G, A)^2 \left\{ \frac{f_{GA} + \frac{1}{2}f_{gA}}{f_A} \right\} \\
& + \\
& m_{GA}S(G, a)^2 \left\{ \frac{\frac{1}{2}f_{Ga} + \frac{1}{4}f_{ga}}{f_a} \right\} \\
& + \\
& 2m_{GA}S(G, A)S(G, a) \left\{ \frac{f_{GA} + \frac{1}{2}f_{gA}}{f_A} \frac{\Pi_{Aa}}{\Pi_{Aa} + \Pi_{aA}} + \frac{\frac{1}{2}f_{Ga} + \frac{1}{4}f_{ga}}{f_a} \frac{\Pi_{aA}}{\Pi_{Aa} + \Pi_{aA}} \right\}
\end{aligned}$$

$$\begin{aligned}
& + \\
& m_{Ga}S(G, A)^2 \left\{ \frac{\frac{1}{2}f_{GA} + \frac{1}{4}f_{gA}}{f_A} \right\} \\
& + \\
& m_{Ga}S(G, a)^2 \{0\} \\
& + \\
& 2m_{Ga}S(G, A)S(G, a) \left\{ \frac{\frac{1}{2}f_{GA} + \frac{1}{4}f_{gA}}{f_A} \frac{\Pi_{Aa}}{\Pi_{Aa} + \Pi_{aA}} \right\} \\
& + \\
& m_{gA}S(g, A)^2 \left\{ \frac{\frac{1}{2}f_{GA}}{f_A} \right\} \\
& + \\
& m_{gA}S(g, a)^2 \left\{ \frac{\frac{1}{4}f_{Ga}}{f_a} \right\} \\
& + \\
& 2m_{gA}S(g, A)S(g, a) \left\{ \frac{\frac{1}{2}f_{GA}}{f_A} \frac{\Pi_{Aa}}{\Pi_{Aa} + \Pi_{aA}} + \frac{\frac{1}{4}f_{Ga}}{f_a} \frac{\Pi_{aA}}{\Pi_{Aa} + \Pi_{aA}} \right\} \\
& + \\
& m_{ga}S(g, A)^2 \left\{ \frac{\frac{1}{4}f_{GA}}{f_A} \right\} \\
& + \\
& m_{ga}S(g, a)^2 \{0\} \\
& + \\
& 2m_{ga}S(g, A)S(g, a) \left\{ \frac{\frac{1}{4}f_{GA}}{f_A} \frac{\Pi_{Aa}}{\Pi_{Aa} + \Pi_{aA}} \right\}
\end{aligned}$$

$$\begin{aligned}
m'_{Ga} = & \\
& m_{GA}S(G, A)^2 \{0\} \\
& + \\
& m_{GA}S(G, a)^2 \left\{ \frac{\frac{1}{2}f_{Ga} + \frac{1}{4}f_{ga}}{f_a} \right\} \\
& + \\
& 2m_{GA}S(G, A)S(G, a) \left\{ \frac{\frac{1}{2}f_{Ga} + \frac{1}{4}f_{ga}}{f_a} \frac{\Pi_{aA}}{\Pi_{Aa} + \Pi_{aA}} \right\} \\
& + \\
& m_{Ga}S(G, A)^2 \left\{ \frac{\frac{1}{2}f_{GA} + \frac{1}{4}f_{gA}}{f_A} \right\} \\
& + \\
& m_{Ga}S(G, a)^2 \left\{ \frac{f_{Ga} + \frac{1}{2}f_{ga}}{f_a} \right\} \\
& + \\
& 2m_{Ga}S(G, A)S(G, a) \left\{ \frac{\frac{1}{2}f_{GA} + \frac{1}{4}f_{gA}}{f_A} \frac{\Pi_{Aa}}{\Pi_{Aa} + \Pi_{aA}} + \frac{f_{Ga} + \frac{1}{2}f_{ga}}{f_a} \frac{\Pi_{aA}}{\Pi_{Aa} + \Pi_{aA}} \right\} \\
& + \\
& m_{gA}S(g, A)^2 \{0\} \\
& + \\
& m_{gA}S(g, a)^2 \left\{ \frac{\frac{1}{4}f_{Ga}}{f_a} \right\} \\
& +
\end{aligned}$$

$$\begin{aligned}
& 2m_{gA}S(g, A)S(g, a) \left\{ \frac{\frac{1}{4}f_{Ga}}{f_a} \frac{\Pi_{aA}}{\Pi_{Aa} + \Pi_{aA}} \right\} \\
& + \\
& m_{ga}S(g, A)^2 \left\{ \frac{\frac{1}{4}f_{GA}}{f_A} \right\} \\
& + \\
& m_{ga}S(g, a)^2 \left\{ \frac{\frac{1}{2}f_{Ga}}{f_a} \right\} \\
& + \\
& 2m_{ga}S(g, A)S(g, a) \left\{ \frac{\frac{1}{4}f_{GA}}{f_A} \frac{\Pi_{Aa}}{\Pi_{Aa} + \Pi_{aA}} + \frac{\frac{1}{2}f_{Ga}}{f_a} \frac{\Pi_{aA}}{\Pi_{Aa} + \Pi_{aA}} \right\} \\
m'_{gA} = & \\
& m_{GA}S(G, A)^2 \left\{ \frac{\frac{1}{2}f_{gA}}{f_A} \right\} \\
& + \\
& m_{GA}S(G, a)^2 \left\{ \frac{\frac{1}{4}f_{ga}}{f_a} \right\} \\
& + \\
& 2m_{GA}S(G, A)S(G, a) \left\{ \frac{\frac{1}{2}f_{gA}}{f_A} \frac{\Pi_{Aa}}{\Pi_{Aa} + \Pi_{aA}} + \frac{\frac{1}{4}f_{ga}}{f_a} \frac{\Pi_{aA}}{\Pi_{Aa} + \Pi_{aA}} \right\} \\
& + \\
& m_{Ga}S(G, A)^2 \left\{ \frac{\frac{1}{4}f_{gA}}{f_A} \right\} \\
& + \\
& m_{Ga}S(G, a)^2 \{0\} \\
& + \\
& 2m_{Ga}S(G, A)S(G, a) \left\{ \frac{\frac{1}{4}f_{gA}}{f_A} \frac{\Pi_{Aa}}{\Pi_{Aa} + \Pi_{aA}} \right\} \\
& + \\
& m_{gA}S(g, A)^2 \left\{ \frac{\frac{1}{2}f_{GA} + f_{gA}}{f_A} \right\} \\
& + \\
& m_{gA}S(g, a)^2 \left\{ \frac{\frac{1}{4}f_{Ga} + \frac{1}{2}f_{ga}}{f_a} \right\} \\
& + \\
& 2m_{gA}S(g, A)S(g, a) \left\{ \frac{\frac{1}{2}f_{GA} + f_{gA}}{f_A} \frac{\Pi_{Aa}}{\Pi_{Aa} + \Pi_{aA}} + \frac{\frac{1}{4}f_{Ga} + \frac{1}{2}f_{ga}}{f_a} \frac{\Pi_{aA}}{\Pi_{Aa} + \Pi_{aA}} \right\} \\
& + \\
& m_{ga}S(g, A)^2 \left\{ \frac{\frac{1}{4}f_{GA} + \frac{1}{2}f_{gA}}{f_A} \right\} \\
& + \\
& m_{ga}S(g, a)^2 \{0\} \\
& + \\
& 2m_{ga}S(g, A)S(g, a) \left\{ \frac{\frac{1}{4}f_{GA} + \frac{1}{2}f_{gA}}{f_A} \frac{\Pi_{Aa}}{\Pi_{Aa} + \Pi_{aA}} \right\} \\
m'_{ga} = & \\
& m_{GA}S(G, A)^2 \{0\} \\
& +
\end{aligned}$$

$$\begin{aligned}
& m_{GA}S(G, a)^2 \left\{ \frac{\frac{1}{4}f_{ga}}{f_a} \right\} \\
& + \\
& 2m_{GA}S(G, A)S(G, a) \left\{ \frac{\frac{1}{4}f_{ga}}{f_a} \frac{\Pi_{aA}}{\Pi_{Aa} + \Pi_{aA}} \right\} \\
& + \\
& m_{Ga}S(G, A)^2 \left\{ \frac{\frac{1}{4}f_{gA}}{f_A} \right\} \\
& + \\
& m_{Ga}S(G, a)^2 \left\{ \frac{\frac{1}{2}f_{ga}}{f_a} \right\} \\
& + \\
& 2m_{Ga}S(G, A)S(G, a) \left\{ \frac{\frac{1}{4}f_{gA}}{f_A} \frac{\Pi_{Aa}}{\Pi_{Aa} + \Pi_{aA}} + \frac{\frac{1}{2}f_{ga}}{f_a} \frac{\Pi_{aA}}{\Pi_{Aa} + \Pi_{aA}} \right\} \\
& + \\
& m_{gA}S(g, A)^2 \{0\} \\
& + \\
& m_{gA}S(g, a)^2 \left\{ \frac{\frac{1}{4}f_{Ga} + \frac{1}{2}f_{ga}}{f_a} \right\} \\
& + \\
& 2m_{gA}S(g, A)S(g, a) \left\{ \frac{\frac{1}{4}f_{Ga} + \frac{1}{2}f_{ga}}{f_a} \frac{\Pi_{aA}}{\Pi_{Aa} + \Pi_{aA}} \right\} \\
& + \\
& m_{ga}S(g, A)^2 \left\{ \frac{\frac{1}{4}f_{GA} + \frac{1}{2}f_{gA}}{f_A} \right\} \\
& + \\
& m_{ga}S(g, a)^2 \left\{ \frac{\frac{1}{2}f_{Ga} + f_{ga}}{f_a} \right\} \\
& + \\
& 2m_{ga}S(g, A)S(g, a) \left\{ \frac{\frac{1}{4}f_{GA} + \frac{1}{2}f_{gA}}{f_A} \frac{\Pi_{Aa}}{\Pi_{Aa} + \Pi_{aA}} + \frac{\frac{1}{2}f_{Ga} + f_{ga}}{f_a} \frac{\Pi_{aA}}{\Pi_{Aa} + \Pi_{aA}} \right\}
\end{aligned}$$

The female recurrence relations are again defined using  $N'$ , the total number of female children in the next generation.  $N'$  is now

$$\begin{aligned}
N' \equiv & \{m_GS(G, A)^2 + m_gS(g, A)^2\} \{2\Pi_{AA}\} \\
& + \{m_GS(G, a)^2 + m_gS(g, a)^2\} \{2\Pi_{aa}\} \\
& + 2\{m_GS(G, A)S(G, a) + m_gS(g, A)S(g, a)\} \{\Pi_{Aa} + \Pi_{aA}\}
\end{aligned}$$

The female recurrence relations are:

$$\begin{aligned}
f'_{GA} = & \\
& m_{GA}S(G, A)^2 \left\{ \frac{f_{GA} + \frac{1}{2}f_{gA}}{f_A} \left( \frac{2\Pi_{AA}}{N'} \right) \right\} \\
& + \\
& m_{GA}S(G, a)^2 \left\{ \frac{\frac{1}{2}f_{Ga} + \frac{1}{4}f_{ga}}{f_a} \left( \frac{2\Pi_{aa}}{N'} \right) \right\} \\
& + \\
& 2m_{GA}S(G, A)S(G, a) \left\{ \frac{f_{GA} + \frac{1}{2}f_{gA}}{f_A} \left( \frac{\Pi_{Aa}}{N'} \right) + \frac{\frac{1}{2}f_{Ga} + \frac{1}{4}f_{ga}}{f_a} \left( \frac{\Pi_{aA}}{N'} \right) \right\}
\end{aligned}$$

$$\begin{aligned}
& + \\
& m_{Ga}S(G, A)^2 \left\{ \frac{\frac{1}{2}f_{GA} + \frac{1}{4}f_{gA}}{f_A} \left( \frac{2\Pi_{AA}}{N'} \right) \right\} \\
& + \\
& m_{Ga}S(G, a)^2 \{0\} \\
& + \\
& 2m_{Ga}S(G, A)S(G, a) \left\{ \frac{\frac{1}{2}f_{GA} + \frac{1}{4}f_{gA}}{f_A} \left( \frac{\Pi_{Aa}}{N'} \right) \right\} \\
& + \\
& m_{gA}S(g, A)^2 \left\{ \frac{\frac{1}{2}f_{GA}}{f_A} \left( \frac{2\Pi_{AA}}{N'} \right) \right\} \\
& + \\
& m_{gA}S(g, a)^2 \left\{ \frac{\frac{1}{4}f_{Ga}}{f_a} \left( \frac{2\Pi_{aa}}{N'} \right) \right\} \\
& + \\
& 2m_{gA}S(g, A)S(g, a) \left\{ \frac{\frac{1}{2}f_{GA}}{f_A} \left( \frac{\Pi_{Aa}}{N'} \right) + \frac{\frac{1}{4}f_{Ga}}{f_a} \left( \frac{\Pi_{aA}}{N'} \right) \right\} \\
& + \\
& m_{ga}S(g, A)^2 \left\{ \frac{\frac{1}{4}f_{GA}}{f_A} \left( \frac{2\Pi_{AA}}{N'} \right) \right\} \\
& + \\
& m_{ga}S(g, a)^2 \{0\} \\
& + \\
& 2m_{ga}S(g, A)S(g, a) \left\{ \frac{\frac{1}{4}f_{GA}}{f_A} \left( \frac{\Pi_{Aa}}{N'} \right) \right\}
\end{aligned}$$

$$f'_{Ga} =$$

$$\begin{aligned}
& m_{GA}S(G, A)^2 \{0\} \\
& + \\
& m_{GA}S(G, a)^2 \left\{ \frac{\frac{1}{2}f_{Ga} + \frac{1}{4}f_{ga}}{f_a} \left( \frac{2\Pi_{aa}}{N'} \right) \right\} \\
& + \\
& 2m_{GA}S(G, A)S(G, a) \left\{ \frac{\frac{1}{2}f_{Ga} + \frac{1}{4}f_{ga}}{f_a} \left( \frac{\Pi_{aA}}{N'} \right) \right\} \\
& + \\
& m_{Ga}S(G, A)^2 \left\{ \frac{\frac{1}{2}f_{GA} + \frac{1}{4}f_{gA}}{f_A} \left( \frac{2\Pi_{AA}}{N'} \right) \right\} \\
& + \\
& m_{Ga}S(G, a)^2 \left\{ \frac{f_{Ga} + \frac{1}{2}f_{ga}}{f_a} \left( \frac{2\Pi_{aa}}{N'} \right) \right\} \\
& + \\
& 2m_{Ga}S(G, A)S(G, a) \left\{ \frac{\frac{1}{2}f_{GA} + \frac{1}{4}f_{gA}}{f_A} \left( \frac{\Pi_{Aa}}{N'} \right) + \frac{f_{Ga} + \frac{1}{2}f_{ga}}{f_a} \left( \frac{\Pi_{aA}}{N'} \right) \right\} \\
& + \\
& m_{gA}S(g, A)^2 \{0\} \\
& + \\
& m_{gA}S(g, a)^2 \left\{ \frac{\frac{1}{4}f_{Ga}}{f_a} \left( \frac{2\Pi_{aa}}{N'} \right) \right\} \\
& +
\end{aligned}$$

$$\begin{aligned}
& 2m_{gA}S(g, A)S(g, a) \left\{ \frac{\frac{1}{4}f_{Ga}}{f_a} \left( \frac{\Pi_{aA}}{N'} \right) \right\} \\
& + \\
& m_{ga}S(g, A)^2 \left\{ \frac{\frac{1}{4}f_{GA}}{f_A} \left( \frac{2\Pi_{AA}}{N'} \right) \right\} \\
& + \\
& m_{ga}S(g, a)^2 \left\{ \frac{\frac{1}{2}f_{Ga}}{f_a} \left( \frac{2\Pi_{aa}}{N'} \right) \right\} \\
& + \\
& 2m_{ga}S(g, A)S(g, a) \left\{ \frac{\frac{1}{4}f_{GA}}{f_A} \left( \frac{\Pi_{Aa}}{N'} \right) + \frac{\frac{1}{2}f_{Ga}}{f_a} \left( \frac{\Pi_{aA}}{N'} \right) \right\}
\end{aligned}$$

$$f'_{gA} =$$

$$\begin{aligned}
& m_{GA}S(G, A)^2 \left\{ \frac{\frac{1}{2}f_{gA}}{f_A} \left( \frac{2\Pi_{AA}}{N'} \right) \right\} \\
& + \\
& m_{GA}S(G, a)^2 \left\{ \frac{\frac{1}{4}f_{ga}}{f_a} \left( \frac{2\Pi_{aa}}{N'} \right) \right\} \\
& + \\
& 2m_{GA}S(G, A)S(G, a) \left\{ \frac{\frac{1}{2}f_{gA}}{f_A} \left( \frac{\Pi_{Aa}}{N'} \right) + \frac{\frac{1}{4}f_{ga}}{f_a} \left( \frac{\Pi_{aA}}{N'} \right) \right\} \\
& + \\
& m_{Ga}S(G, A)^2 \left\{ \frac{\frac{1}{4}f_{gA}}{f_A} \left( \frac{2\Pi_{AA}}{N'} \right) \right\} \\
& + \\
& m_{Ga}S(G, a)^2 \{0\} \\
& + \\
& 2m_{Ga}S(G, A)S(G, a) \left\{ \frac{\frac{1}{4}f_{gA}}{f_A} \left( \frac{\Pi_{Aa}}{N'} \right) \right\} \\
& + \\
& m_{gA}S(g, A)^2 \left\{ \frac{\frac{1}{2}f_{GA} + f_{gA}}{f_A} \left( \frac{2\Pi_{AA}}{N'} \right) \right\} \\
& + \\
& m_{gA}S(g, a)^2 \left\{ \frac{\frac{1}{4}f_{Ga} + \frac{1}{2}f_{ga}}{f_a} \left( \frac{2\Pi_{aa}}{N'} \right) \right\} \\
& + \\
& 2m_{gA}S(g, A)S(g, a) \left\{ \frac{\frac{1}{2}f_{GA} + f_{gA}}{f_A} \left( \frac{\Pi_{Aa}}{N'} \right) + \frac{\frac{1}{4}f_{Ga} + \frac{1}{2}f_{ga}}{f_a} \left( \frac{\Pi_{aA}}{N'} \right) \right\} \\
& + \\
& m_{ga}S(g, A)^2 \left\{ \frac{\frac{1}{4}f_{GA} + \frac{1}{2}f_{gA}}{f_A} \left( \frac{2\Pi_{AA}}{N'} \right) \right\} \\
& + \\
& m_{ga}S(g, a)^2 \{0\} \\
& + \\
& 2m_{ga}S(g, A)S(g, a) \left\{ \frac{\frac{1}{4}f_{GA} + \frac{1}{2}f_{gA}}{f_A} \left( \frac{\Pi_{Aa}}{N'} \right) \right\}
\end{aligned}$$

$$f'_{ga} =$$

$$\begin{aligned}
& m_{GA}S(G, A)^2 \{0\} \\
& +
\end{aligned}$$



$$\begin{aligned}
& m_{GA}S(G, a)^2 \left\{ \frac{\frac{1}{4}f_{ga}}{f_a} \left( \frac{2\Pi_{aa}}{N'} \right) \right\} \\
& + \\
& 2m_{GA}S(G, A)S(G, a) \left\{ \frac{\frac{1}{4}f_{ga}}{f_a} \left( \frac{\Pi_{aA}}{N'} \right) \right\} \\
& + \\
& m_{Ga}S(G, A)^2 \left\{ \frac{\frac{1}{4}f_{gA}}{f_A} \left( \frac{2\Pi_{AA}}{N'} \right) \right\} \\
& + \\
& m_{Ga}S(G, a)^2 \left\{ \frac{\frac{1}{2}f_{ga}}{f_a} \left( \frac{2\Pi_{aa}}{N'} \right) \right\} \\
& + \\
& 2m_{Ga}S(G, A)S(G, a) \left\{ \frac{\frac{1}{4}f_{gA}}{f_A} \left( \frac{\Pi_{Aa}}{N'} \right) + \frac{\frac{1}{2}f_{ga}}{f_a} \left( \frac{\Pi_{aA}}{N'} \right) \right\} \\
& + \\
& m_{gA}S(g, A)^2 \{0\} \\
& + \\
& m_{gA}S(g, a)^2 \left\{ \frac{\frac{1}{4}f_{Ga} + \frac{1}{2}f_{ga}}{f_a} \left( \frac{2\Pi_{aa}}{N'} \right) \right\} \\
& + \\
& 2m_{gA}S(g, A)S(g, a) \left\{ \frac{\frac{1}{4}f_{Ga} + \frac{1}{2}f_{ga}}{f_a} \left( \frac{\Pi_{aA}}{N'} \right) \right\} \\
& + \\
& m_{ga}S(g, A)^2 \left\{ \frac{\frac{1}{4}f_{GA} + \frac{1}{2}f_{gA}}{f_A} \left( \frac{2\Pi_{AA}}{N'} \right) \right\} \\
& + \\
& m_{ga}S(g, a)^2 \left\{ \frac{\frac{1}{2}f_{Ga} + f_{ga}}{f_a} \left( \frac{2\Pi_{aa}}{N'} \right) \right\} \\
& + \\
& 2m_{ga}S(g, A)S(g, a) \left\{ \frac{\frac{1}{4}f_{GA} + \frac{1}{2}f_{gA}}{f_A} \left( \frac{\Pi_{Aa}}{N'} \right) + \frac{\frac{1}{2}f_{Ga} + f_{ga}}{f_a} \left( \frac{\Pi_{aA}}{N'} \right) \right\}
\end{aligned}$$

## 5 An alternative exposition

An alternative exposition that may be easier to follow is in terms of "couples" or "families". A "couple" or "family" is a male and his wife(s). The total number of families is normalized to 1. The composition of the family is in the subscripts with the husband's genotype followed by the wives' genotypes, e.g.,  $C_{GA;ga,Ga}$  denotes the share of families where the husband is genotype  $GA$ , one wife is  $ga$  and the other wife is  $Ga$ .

This approach lets us distinguish more clearly between the adoption step and the reproduction step. In each period  $t$ , we first see adoptions (dating games) by males; the results of this is families. Then foraging, reproduction, and dispersals of females take place.

Here, in painful detail, are the equations for the shares of all possible configurations of families. Each has 3 terms: the relevant male share; the probabilities that a male of that

phenotype ( $G$  or  $g$ ) finds himself with females of type  $A$  and/or type  $a$  as mates; the shares of females of these types carrying a  $G$  or a  $g$  gene.

1.  $GA$  males:

$$C_{GA;GA,GA} = m_{GA}S(G, A)^2 \left\{ \frac{f_{GA}}{f_A} \right\}^2$$

$$C_{GA;GA,gA} = 2m_{GA}S(G, A)^2 \left\{ \frac{f_{GA}}{f_A} \right\} \left\{ \frac{f_{gA}}{f_A} \right\}$$

$$C_{GA;gA,gA} = m_{GA}S(G, A)^2 \left\{ \frac{f_{gA}}{f_A} \right\}^2$$

$$C_{GA;Ga,Ga} = m_{GA}S(G, a)^2 \left\{ \frac{f_{Ga}}{f_a} \right\}^2$$

$$C_{GA;Ga,gA} = 2m_{GA}S(G, a)^2 \left\{ \frac{f_{Ga}}{f_a} \right\} \left\{ \frac{f_{ga}}{f_a} \right\}$$

$$C_{GA;ga,gA} = m_{GA}S(G, a)^2 \left\{ \frac{f_{ga}}{f_a} \right\}^2$$

$$C_{GA;GA,Ga} = m_{GA}S(G, A)S(G, a) \left\{ \frac{f_{GA}}{f_A} \right\} \left\{ \frac{f_{Ga}}{f_a} \right\}$$

$$C_{GA;GA,gA} = m_{GA}S(G, A)S(G, a) \left\{ \frac{f_{GA}}{f_A} \right\} \left\{ \frac{f_{ga}}{f_a} \right\}$$

$$C_{GA;gA,Ga} = m_{GA}S(G, A)S(G, a) \left\{ \frac{f_{gA}}{f_A} \right\} \left\{ \frac{f_{Ga}}{f_a} \right\}$$

$$C_{GA;gA,gA} = m_{GA}S(G, A)S(G, a) \left\{ \frac{f_{gA}}{f_A} \right\} \left\{ \frac{f_{ga}}{f_a} \right\}$$

2.  $Ga$  males (because the  $Ga$  males don't express the  $a$  gene, these vary from the ones for  $GA$  males only in the first term, i.e., the  $m$  shares):

$$C_{Ga;GA,GA} = m_{Ga}S(G, A)^2 \left\{ \frac{f_{GA}}{f_A} \right\}^2$$

$$C_{Ga;GA,gA} = m_{Ga}S(G, A)^2 \left\{ \frac{f_{GA}}{f_A} \right\} \left\{ \frac{f_{gA}}{f_A} \right\}$$

$$C_{Ga;gA,gA} = m_{Ga}S(G, A)^2 \left\{ \frac{f_{gA}}{f_A} \right\}^2$$

$$C_{Ga;Ga,Ga} = m_{Ga}S(G, a)^2 \left\{ \frac{f_{Ga}}{f_a} \right\}^2$$

$$C_{Ga;Ga,ga} = m_{Ga}S(G, a)^2 \left\{ \frac{f_{Ga}}{f_a} \right\} \left\{ \frac{f_{ga}}{f_a} \right\}$$

$$C_{Ga;ga,ga} = m_{Ga}S(G, a)^2 \left\{ \frac{f_{ga}}{f_a} \right\}^2$$

$$C_{Ga;GA,Ga} = m_{Ga}S(G, A)S(G, a) \left\{ \frac{f_{GA}}{f_A} \right\} \left\{ \frac{f_{Ga}}{f_a} \right\}$$

$$C_{Ga;GA,ga} = m_{Ga}S(G, A)S(G, a) \left\{ \frac{f_{GA}}{f_A} \right\} \left\{ \frac{f_{ga}}{f_a} \right\}$$

$$C_{Ga;gA,Ga} = m_{Ga}S(G, A)S(G, a) \left\{ \frac{f_{gA}}{f_A} \right\} \left\{ \frac{f_{Ga}}{f_a} \right\}$$

$$C_{Ga;gA,ga} = m_{Ga}S(G, A)S(G, a) \left\{ \frac{f_{gA}}{f_A} \right\} \left\{ \frac{f_{ga}}{f_a} \right\}$$

3.  $gA$  males (now both the  $m$  shares and the matching function  $S$  change):

$$C_{gA;GA,GA} = m_{gA}S(g, A)^2 \left\{ \frac{f_{GA}}{f_A} \right\}^2$$

$$C_{gA;GA,gA} = m_{gA}S(g, A)^2 \left\{ \frac{f_{GA}}{f_A} \right\} \left\{ \frac{f_{gA}}{f_A} \right\}$$

$$C_{gA;gA,gA} = m_{gA}S(g, A)^2 \left\{ \frac{f_{gA}}{f_A} \right\}^2$$

$$C_{gA;Ga,Ga} = m_{gA}S(g, a)^2 \left\{ \frac{f_{Ga}}{f_a} \right\}^2$$

$$C_{gA;Ga,ga} = m_{gA}S(g, a)^2 \left\{ \frac{f_{Ga}}{f_a} \right\} \left\{ \frac{f_{ga}}{f_a} \right\}$$

$$C_{gA;ga,ga} = m_{gA}S(g, a)^2 \left\{ \frac{f_{ga}}{f_a} \right\}^2$$

$$C_{gA;GA,Ga} = m_{gA}S(g, A)S(g, a) \left\{ \frac{f_{GA}}{f_A} \right\} \left\{ \frac{f_{Ga}}{f_a} \right\}$$

$$C_{gA;GA,ga} = m_{gA}S(g, A)S(g, a) \left\{ \frac{f_{GA}}{f_A} \right\} \left\{ \frac{f_{ga}}{f_a} \right\}$$

$$C_{gA;gA,Ga} = m_{gA}S(g, A)S(g, a) \left\{ \frac{f_{gA}}{f_A} \right\} \left\{ \frac{f_{Ga}}{f_a} \right\}$$

$$C_{gA;gA,ga} = m_{gA}S(g, A)S(g, a) \left\{ \frac{f_{gA}}{f_A} \right\} \left\{ \frac{f_{ga}}{f_a} \right\}$$

4. *ga* males:

$$C_{ga;GA,GA} = m_{ga} S(g, A)^2 \left\{ \frac{f_{GA}}{f_A} \right\}^2$$

$$C_{ga;GA,gA} = m_{ga} S(g, A)^2 \left\{ \frac{f_{GA}}{f_A} \right\} \left\{ \frac{f_{gA}}{f_A} \right\}$$

$$C_{ga;gA,gA} = m_{ga} S(g, A)^2 \left\{ \frac{f_{gA}}{f_A} \right\}^2$$

$$C_{ga;Ga,Ga} = m_{ga} S(g, a)^2 \left\{ \frac{f_{Ga}}{f_a} \right\}^2$$

$$C_{ga;Ga,ga} = m_{ga} S(g, a)^2 \left\{ \frac{f_{Ga}}{f_a} \right\} \left\{ \frac{f_{ga}}{f_a} \right\}$$

$$C_{ga;ga,ga} = m_{ga} S(g, a)^2 \left\{ \frac{f_{ga}}{f_a} \right\}^2$$

$$C_{ga;GA,Ga} = m_{ga} S(g, A) S(g, a) \left\{ \frac{f_{GA}}{f_A} \right\} \left\{ \frac{f_{Ga}}{f_a} \right\}$$

$$C_{ga;GA,ga} = m_{ga} S(g, A) S(g, a) \left\{ \frac{f_{GA}}{f_A} \right\} \left\{ \frac{f_{ga}}{f_a} \right\}$$

$$C_{ga;gA,Ga} = m_{ga} S(g, A) S(g, a) \left\{ \frac{f_{gA}}{f_A} \right\} \left\{ \frac{f_{Ga}}{f_a} \right\}$$

$$C_{ga;gA,ga} = m_{ga} S(g, A) S(g, a) \left\{ \frac{f_{gA}}{f_A} \right\} \left\{ \frac{f_{ga}}{f_a} \right\}$$

Next, we write out the mail recurrence relations in terms of families. The share of each type of family is weighted by the contribution to the male genotype. This has two components, consisting of the contribution of the first female and the contribution of the second female. These contributions in turn consist of the share of that female's children that contributes to the male genotype weighted by the female's share of total fecundity in the family. In *AA* and *aa* female pairings, these last shares are always  $\frac{1}{2}$ , since the two females have identical payoffs. In *Aa* and *aA* pairings, the *A* female has a smaller share because she is exploited by the *a* female.

This structure corresponds to how the male children "fight it out" for who gets to be the adult male in the next generation. This competition is intra-family only. In effect, we taking the probability that a male of a specific genotype will be the winner in a particular type of family, and summing these across all families to obtain the share of families in the next generation headed by a male of this genotype.

The male recurrence relations are:

$$\begin{aligned}
m'_{GA} = & C_{GA;GA,GA} \left\{ \left(1 \times \frac{1}{2}\right) + \left(1 \times \frac{1}{2}\right) \right\} + C_{GA;GA,gA} \left\{ \left(1 \times \frac{1}{2}\right) + \left(\frac{1}{2} \times \frac{1}{2}\right) \right\} \\
& + \\
& C_{GA;Ga,Ga} \left\{ \left(\frac{1}{2} \times \frac{1}{2}\right) + \left(\frac{1}{2} \times \frac{1}{2}\right) \right\} + C_{GA;Ga,ga} \left\{ \left(\frac{1}{2} \times \frac{1}{2}\right) + \left(0 \times \frac{1}{2}\right) \right\} \\
& + \\
& C_{GA;GA,Ga} \left\{ \frac{\Pi_{Aa}}{\Pi_{Aa} + \Pi_{aA}} + \frac{1}{2} \frac{\Pi_{aA}}{\Pi_{Aa} + \Pi_{aA}} \right\} + C_{GA;GA,ga} \left\{ \frac{\Pi_{Aa}}{\Pi_{Aa} + \Pi_{aA}} + \frac{1}{4} \frac{\Pi_{aA}}{\Pi_{Aa} + \Pi_{aA}} \right\} \\
& + \\
& C_{GA;gA,Ga} \left\{ \frac{1}{2} \frac{\Pi_{Aa}}{\Pi_{Aa} + \Pi_{aA}} + \frac{1}{2} \frac{\Pi_{aA}}{\Pi_{Aa} + \Pi_{aA}} \right\} + C_{GA;gA,ga} \left\{ \frac{1}{2} \frac{\Pi_{Aa}}{\Pi_{Aa} + \Pi_{aA}} + \frac{1}{4} \frac{\Pi_{aA}}{\Pi_{Aa} + \Pi_{aA}} \right\} \\
& + \\
& C_{Ga;GA,GA} \left\{ \left(\frac{3}{4} \times \frac{1}{2}\right) + \left(\frac{3}{4} \times \frac{1}{2}\right) \right\} + C_{Ga;GA,gA} \left\{ \left(\frac{1}{2} \times \frac{1}{2}\right) + \left(\frac{1}{2} \times \frac{1}{2}\right) \right\} \\
& + \\
& C_{Ga;Ga,Ga} \left\{ \left(0 \times \frac{1}{2}\right) + \left(0 \times \frac{1}{2}\right) \right\} + C_{Ga;Ga,ga} \left\{ \left(0 \times \frac{1}{2}\right) + \left(0 \times \frac{1}{2}\right) \right\} \\
& + \\
& C_{Ga;GA,Ga} \left\{ \frac{1}{2} \frac{\Pi_{Aa}}{\Pi_{Aa} + \Pi_{aA}} + \{0\} \frac{\Pi_{aA}}{\Pi_{Aa} + \Pi_{aA}} \right\} + C_{Ga;GA,ga} \left\{ \frac{1}{2} \frac{\Pi_{Aa}}{\Pi_{Aa} + \Pi_{aA}} + \{0\} \frac{\Pi_{aA}}{\Pi_{Aa} + \Pi_{aA}} \right\} \\
& + \\
& C_{Ga;gA,Ga} \left\{ \frac{1}{4} \frac{\Pi_{Aa}}{\Pi_{Aa} + \Pi_{aA}} + \{0\} \frac{\Pi_{aA}}{\Pi_{Aa} + \Pi_{aA}} \right\} + C_{Ga;gA,ga} \left\{ \frac{1}{4} \frac{\Pi_{Aa}}{\Pi_{Aa} + \Pi_{aA}} + \{0\} \frac{\Pi_{aA}}{\Pi_{Aa} + \Pi_{aA}} \right\} \\
& + \\
& C_{gA;GA,GA} \left\{ \left(\frac{1}{2} \times \frac{1}{2}\right) + \left(\frac{1}{2} \times \frac{1}{2}\right) \right\} + C_{gA;GA,gA} \left\{ \left(\frac{1}{2} \times \frac{1}{2}\right) + \left(0 \times \frac{1}{2}\right) \right\} \\
& + \\
& C_{gA;Ga,Ga} \left\{ \left(\frac{1}{4} \times \frac{1}{2}\right) + \left(\frac{1}{4} \times \frac{1}{2}\right) \right\} + C_{gA;Ga,ga} \left\{ \left(\frac{1}{4} \times \frac{1}{2}\right) + \left(0 \times \frac{1}{2}\right) \right\} \\
& + \\
& C_{gA;GA,Ga} \left\{ \frac{1}{2} \frac{\Pi_{Aa}}{\Pi_{Aa} + \Pi_{aA}} + \frac{1}{4} \frac{\Pi_{aA}}{\Pi_{Aa} + \Pi_{aA}} \right\} + C_{gA;GA,ga} \left\{ \frac{1}{2} \frac{\Pi_{Aa}}{\Pi_{Aa} + \Pi_{aA}} + \{0\} \frac{\Pi_{aA}}{\Pi_{Aa} + \Pi_{aA}} \right\} \\
& + \\
& C_{gA;gA,Ga} \left\{ \frac{1}{4} \frac{\Pi_{Aa}}{\Pi_{Aa} + \Pi_{aA}} + \{0\} \frac{\Pi_{aA}}{\Pi_{Aa} + \Pi_{aA}} \right\} + C_{gA;gA,ga} \left\{ \frac{1}{4} \frac{\Pi_{Aa}}{\Pi_{Aa} + \Pi_{aA}} + \{0\} \frac{\Pi_{aA}}{\Pi_{Aa} + \Pi_{aA}} \right\}
\end{aligned}$$

...and the expressions for the other male genotypes are similar.

The female recurrence relations are different, because all females join a giant adoption pool. In the male case, it is the share of family payoffs (total male children) that counts; in the female case, it is the share of total population payoffs (total female children) that matters.

It may be more intuitive to express the recurrence relations after multiplying both sides by  $N'$ , which is still

$$\begin{aligned}
N' \equiv & \{m_G S(G, A)^2 + m_g S(g, A)^2\} \{2\Pi_{AA}\} \\
& + \{m_G S(G, a)^2 + m_g S(g, a)^2\} \{2\Pi_{aa}\} \\
& + 2\{m_G S(G, A)S(G, a) + m_g S(g, A)S(g, a)\} \{\Pi_{Aa} + \Pi_{aA}\}
\end{aligned}$$

This means the equations are for the total numbers of female children of that genotype, and dividing through by  $N'$  would give their shares.

$$\begin{aligned}
N' f'_{GA} = & C_{GA;GA,GA} \{(1 \times \Pi_{AA}) + (1 \times \Pi_{AA})\} + C_{GA;GA,gA} \{(1 \times \Pi_{AA}) + (\frac{1}{2} \times \Pi_{AA})\} \\
& + \\
& C_{GA;Ga,Ga} \{(\frac{1}{2} \times \Pi_{aa}) + (\frac{1}{2} \times \Pi_{AA})\} + C_{GA;Ga,ga} \{(\frac{1}{2} \times \Pi_{AA}) + (0 \times \Pi_{AA})\} \\
& + \\
& C_{GA;GA,Ga} \{\Pi_{Aa} + \frac{1}{2} \Pi_{aA}\} + C_{GA;GA,ga} \{\Pi_{Aa} + \frac{1}{4} \Pi_{aA}\} \\
& + \\
& C_{GA;gA,Ga} \{\frac{1}{2} \Pi_{Aa} + \frac{1}{2} \Pi_{aA}\} + C_{GA;gA,ga} \{\frac{1}{2} \Pi_{Aa} + \frac{1}{4} \Pi_{aA}\} \\
& + \\
& C_{Ga;GA,GA} \{(\frac{3}{4} \times \Pi_{AA}) + (\frac{3}{4} \times \Pi_{AA})\} + C_{Ga;GA,gA} \{(\frac{1}{2} \times \Pi_{AA}) + (\frac{1}{2} \times \Pi_{AA})\} \\
& + \\
& C_{Ga;Ga,Ga} \{(0 \times \Pi_{aa}) + (0 \times \Pi_{aa})\} + C_{Ga;Ga,ga} \{(0 \times \Pi_{aa}) + (0 \times \Pi_{aa})\} \\
& + \\
& C_{Ga;GA,Ga} \{\frac{1}{2} \Pi_{Aa} + \{0\} \Pi_{aA}\} + C_{Ga;GA,ga} \{\frac{1}{2} \Pi_{Aa} + \{0\} \Pi_{aA}\} \\
& + \\
& C_{Ga;gA,Ga} \{\frac{1}{4} \Pi_{Aa} + \{0\} \Pi_{aA}\} + C_{Ga;gA,ga} \{\frac{1}{4} \Pi_{Aa} + \{0\} \Pi_{aA}\} \\
& + \\
& C_{gA;GA,GA} \{(\frac{1}{2} \times \Pi_{AA}) + (\frac{1}{2} \times \Pi_{AA})\} + C_{gA;GA,gA} \{(\frac{1}{2} \times \Pi_{AA}) + (0 \times \Pi_{AA})\} \\
& + \\
& C_{gA;Ga,Ga} \{(\frac{1}{4} \times \Pi_{aa}) + (\frac{1}{4} \times \Pi_{aa})\} + C_{gA;Ga,ga} \{(\frac{1}{4} \times \Pi_{aa}) + (0 \times \Pi_{aa})\} \\
& + \\
& C_{gA;GA,Ga} \{\frac{1}{2} \Pi_{Aa} + \frac{1}{4} \Pi_{aA}\} + C_{gA;GA,ga} \{\frac{1}{2} \Pi_{Aa} + \{0\} \Pi_{aA}\} \\
& + \\
& C_{gA;gA,Ga} \{\frac{1}{4} \Pi_{Aa} + \{0\} \Pi_{aA}\} + C_{gA;gA,ga} \{\frac{1}{4} \Pi_{Aa} + \{0\} \Pi_{aA}\}
\end{aligned}$$

...and the expressions for the other female genotypes are similar.

Collecting terms, simplifying, and substituting out the expressions for the types of families  $C$  generates the simplified recurrence relations in the previous section.

But perhaps what we are really interested in is the composition of families, and we should be presenting results in terms of things like  $C_G$  and  $C_A$ .