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# Intragenomic Conflict over Bet-Hedging

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## Supplementary Information

### S.1 The Model

We recapitulate briefly the derivation of equation (1.2) from the main text to explain the notation and to clarify the assumptions that go into that derivation. For ease of comparison, we follow the nomenclature of Frank and Slatkin. The mean reproductive success of alleles  $A_1$  and  $A_2$ , and of the population as a whole can be written as

$$\begin{aligned} R_1 &= \frac{1}{Nq_1} \sum_{i=1}^{Nq_1} (\mu_1 + \alpha_{1i}) = \mu_1 + \alpha_1 \\ R_2 &= \frac{1}{Nq_2} \sum_{i=1}^{Nq_2} (\mu_2 + \alpha_{2i}) = \mu_2 + \alpha_2 \\ \bar{R} &= q_1 R_1 + q_2 R_2. \end{aligned} \tag{S1}$$

Here,  $\mu_k$  are the expected mean reproduction for allele  $k$ ,  $\alpha_{ki}$  are the deviation of the reproductive success of  $i^{\text{th}}$  individual carrying allele  $k$  from this mean, and  $\alpha_k \equiv \text{Mean}[\alpha_{ki}]$  represent the mean deviation of the realized reproductive success from the expectation for allele  $k$ .

The frequency  $q'_1$  of the  $A_1$  allele in the next generation is given by  $q'_1 = q_1 R_1 / \bar{R}$ . The expected change in the frequency of the  $A_1$  allele, is simply  $E[\Delta q_1] = E[q'_1] - q_1$ . Substituting the relations from equations (S1) and using  $q_1 + q_2 = 1$ , we have

$$E[\Delta q_1] = E \left[ \frac{q_1 q_2 [(\mu_1 + \alpha_1) - (\mu_2 + \alpha_2)]}{q_1 (\mu_1 + \alpha_1) + q_2 (\mu_2 + \alpha_2)} \right]. \tag{S2}$$

Without loss of generality, Frank and Slatkin set  $q_1 \mu_1 + q_2 \mu_2 = 1$ , which corresponds to rescaling the  $\mu$  and  $\alpha$  by the expected reproductive success of the population. Equation (S2) then reduces to

$$E[\Delta q_1] = q_1 q_2 E \left[ \frac{(\mu_1 + \alpha_1) - (\mu_2 + \alpha_2)}{1 + q_1 \alpha_1 + q_2 \alpha_2} \right]. \tag{S3}$$

The trouble in evaluating equation (S3) comes from the fact that there is not a general solution for the expectation of a ratio. However, provided that the overall stochastic fluctuation in reproductive output is small relative to the total population size ( $\Delta N \ll N$ , or equivalently,  $q_1 \alpha_1 + q_2 \alpha_2 \ll 1$ ), we can approximate it as

$$E[\Delta q_1] = q_1 q_2 E [(\mu_1 - \mu_2 + \alpha_1 - \alpha_2)(1 - (q_1 \alpha_1 + q_2 \alpha_2) + (q_1 \alpha_1 + q_2 \alpha_2)^2)] + O(\alpha^3). \tag{S4}$$

One potentially confusing aspect of this derivation arises from the fact that we are considering two different types of mean value. The first, represented by  $\alpha_1$  and  $\alpha_2$ , is an average across individuals, but limited to a single realization of the stochastic process undergone by the population as a whole. The second, represented by the expectation operator  $E[\dots]$ , is a mean taken over many hypothetical realizations of the reproductive process of the entire population. While  $\alpha_1$  and  $\alpha_2$  could each take on either positive or negative values in any single realization, these quantities are defined such that  $E[\alpha_1] = E[\alpha_2] = 0$ . The higher moments of these fluctuations are, however, not zero:

$$\begin{aligned} E[\alpha_1^2] &= \text{Var}[R_1] = \rho_1 \sigma_1^2 \\ E[\alpha_2^2] &= \text{Var}[R_2] = \rho_2 \sigma_2^2 \\ E[\alpha_1 \alpha_2] &= \text{Cov}[R_1, R_2] = \rho_{12} \sigma_1 \sigma_2, \end{aligned} \quad (\text{S5})$$

where  $\text{Var}[R_k]$  and  $\text{Cov}[R_1, R_2]$  represent the variance of  $R_k$  and the covariance of  $R_1$  with  $R_2$ , respectively.

With this in mind, we can now take the expectation of each of the terms in equation (S4). We can also simplify notation by introducing  $\Delta\mu = \mu_1 - \mu_2$ . This gives

$$E[\Delta q_1] = q_1 q_2 (\Delta\mu + q_1 (q_1 \Delta\mu - 1) E[\alpha_1^2]) + (q_1 - q_2 + 2 q_1 q_2 \Delta\mu) E[\alpha_1 \alpha_2] + q_2 (q_2 \Delta\mu + 1) E[\alpha_2^2] + O(\alpha^3). \quad (\text{S6})$$

To arrive at their final expression, Frank and Slatkin make the further assumption that  $\Delta\mu$  is small. Equation (S4) then reduces to

$$E[\Delta\mu] = q_1 q_2 (\Delta\mu - q_1 E[\alpha_1^2]) + (q_1 - q_2) E[\alpha_1 \alpha_2] + q_2 E[\alpha_2^2] + O(\alpha^3, \alpha^2 \Delta\mu). \quad (\text{S7})$$

## S.2 Diploid Model

For the diploid analog of the Frank and Slatkin model, we begin with the reproductive success of the three genotypes. For simplicity, we assume a well mixed population at Hardy-Weinberg equilibrium.

$$\begin{aligned} R_{11} &= \frac{1}{N q_1^2} \sum_{i=1}^{N q_1^2} (\mu_{11} + \alpha_{11i}) = \mu_{11} + \alpha_{11} \\ R_{12} &= \frac{1}{2N q_1 q_2} \sum_{i=1}^{2N q_1 q_2} (\mu_{12} + \alpha_{12i}) = \mu_{12} + \alpha_{12} \\ R_{22} &= \frac{1}{N q_2^2} \sum_{i=1}^{N q_2^2} (\mu_{22} + \alpha_{22i}) = \mu_{22} + \alpha_{22}. \end{aligned} \quad (\text{S8})$$

From this, we can calculate the reproductive success of the two alleles:

$$\begin{aligned} R_1 &= q_1 (\mu_{11} + \alpha_{11}) + q_2 (\mu_{12} + 2 \alpha_{12.1}) \\ R_2 &= q_2 (\mu_{22} + \alpha_{22}) + q_1 (\mu_{12} + 2 \alpha_{12.2}) \\ \bar{R} &= q_1 R_1 + q_2 R_2. \end{aligned} \quad (\text{S9})$$

Note that in these expressions, we have split the  $\alpha_{12}$  term into two components. In the previous expression,  $\alpha_{12}$  represents the deviation of the number of offspring from the mean for  $R_{12}$  individuals. Assuming fair segregation, we the expected number of those offspring to carry the  $A_1$  and  $A_2$  alleles will be equal  $\alpha_{12.1}$  represents the excess number of offspring to inherit an  $A_1$  allele from an  $R_{12}$  parent (and  $\alpha_{12.2}$  the excess inheriting  $A_2$ ). The quantity  $\mu_{12}/2 + \alpha_{12.1}$  is distributed as a binomial  $B(\mu_{12} + \alpha_{12}, 1/2)$ , and  $\alpha_{12.2} = \alpha_{12} - \alpha_{12.1}$ .

Now we can write our expression for the expected change in allele frequency

$$E[\Delta q_1] = q_1 q_2 E \left[ \frac{q_1 (\mu_{11} + \alpha_{11}) + q_2 (\mu_{12} + 2 \alpha_{12.1}) - q_1 (\mu_{12} + 2 \alpha_{12.2}) - q_2 (\mu_{22} + \alpha_{22})}{1 + q_1^2 \alpha_{11} + 2 q_1 q_2 \alpha_{12} + q_2^2 \alpha_{22}} \right] \quad (\text{S10})$$

where we have again normalized by the total expected reproductive output by setting  $q_1^2 \mu_{11} + 2q_1 q_2 \mu_{12} + q_2^2 \mu_{22} = 1$ . As in the haploid case, we assume that the fluctuation  $\Delta N$  is small compared with the total population size  $N$ . This allows us to approximate this ratio as

$$E[\Delta q_1] \approx q_1 q_2 \left[ q_1 (\mu_{11} - \mu_{12}) + q_2 (\mu_{12} - \mu_{22}) - q_1^3 E[\alpha_{11}^2] + q_2^3 E[\alpha_{22}^2] - 4q_1 q_2^2 E[\alpha_{12.1} \alpha_{12}] + 4q_1^2 q_2 E[\alpha_{12.2} \alpha_{12}] \right] \quad (\text{S11})$$

We again assume that the reproductive success of different individuals is uncorrelated, and we additionally assume that the population is at Hardy-Weinberg equilibrium. In this case, the non-zero variance and covariance terms are

$$\begin{aligned} E[\alpha_{11}^2] &= \text{Var}[R_{11}] = \rho_{11} \sigma_{11}^2 = \frac{\sigma_{11}^2}{N q_1^2} \\ E[\alpha_{22}^2] &= \text{Var}[R_{22}] = \rho_{22} \sigma_{22}^2 = \frac{\sigma_{22}^2}{N q_2^2} \\ E[\alpha_{12.1} \alpha_{12}] &= E[\alpha_{12.2} \alpha_{12}] = \frac{1}{2} \frac{\sigma_{12}^2}{2N q_1 q_2} \end{aligned} \quad (\text{S12})$$

The approximation for the change in allele frequency then reduces to

$$E[\Delta q_1] \approx q_1 q_2 \left[ q_1 \left( \mu_{11} - \frac{\sigma_{11}^2}{N} - \mu_{12} + \frac{\sigma_{12}^2}{N} \right) + q_2 \left( \mu_{12} - \frac{\sigma_{12}^2}{N} - \mu_{22} + \frac{\sigma_{22}^2}{N} \right) \right] \quad (\text{S13})$$

Note that, as in the haploid analysis, if we define the effective fitness of a genotype as  $w_e = \mu - \sigma^2/N$ , this reduces to the standard formula. Furthermore, if allelic effects on reproductive mean and variance are additive, it reduces to the haploid equation.

### S.3 Genomic Imprinting

Treatment of the general diploid case with genomic imprinting requires the addition of the fact that the two heterozygous genotypes may have different phenotypes. To accommodate this, we modify our notation such that two-number subscripts are ordered, with the first number indicating the identity of the maternally inherited allele and the second number indicating the identity of the paternally inherited allele. For example  $\mu_{12}$  now represents the mean reproductive success of heterozygous individuals whose  $A_1$  allele was maternally inherited and whose  $A_2$  allele was paternally inherited.

We now have four expressions for the mean reproductive output in a given generation:

$$\begin{aligned} R_{11} &= \frac{1}{N q_1^2} \sum_{i=1}^{N q_1^2} (\mu_{11} + \alpha_{11i}) = \mu_{11} + \alpha_{11} \\ R_{12} &= \frac{1}{N q_1 q_2} \sum_{i=1}^{2N q_1 q_2} (\mu_{12} + \alpha_{12i}) = \mu_{12} + \alpha_{12} \\ R_{21} &= \frac{1}{N q_1 q_2} \sum_{i=1}^{2N q_1 q_2} (\mu_{21} + \alpha_{21i}) = \mu_{21} + \alpha_{21} \\ R_{22} &= \frac{1}{N q_2^2} \sum_{i=1}^{N q_2^2} (\mu_{22} + \alpha_{22i}) = \mu_{22} + \alpha_{22}. \end{aligned} \quad (\text{S14})$$

The corresponding expressions for the reproductive output of the two alleles are

$$\begin{aligned} R_1 &= q_1(\mu_{11} + \alpha_{11}) + q_2\left(\frac{\mu_{12}}{2} + \alpha_{12.1} + \frac{\mu_{21}}{2} + \alpha_{21.1}\right) \\ R_2 &= q_2(\mu_{22} + \alpha_{22}) + q_1\left(\frac{\mu_{12}}{2} + \alpha_{12.2} + \frac{\mu_{21}}{2} + \alpha_{21.2}\right) \\ \bar{R} &= q_1R_1 + q_2R_2. \end{aligned} \tag{S15}$$

Once again, we assume that the fluctuations in total reproductive output are small compared with the population size, and that individual reproductive outputs are uncorrelated. The expected change in allele frequency then becomes

$$E[\Delta q_1] \approx q_1q_2 \left[ q_1 \left( \mu_{11} - \frac{\sigma_{11}^2}{N} - \frac{\mu_{12}}{2} + \frac{\sigma_{12}^2}{2N} - \frac{\mu_{21}}{2} + \frac{\sigma_{21}^2}{2N} \right) + q_2 \left( \frac{\mu_{12}}{2} - \frac{\sigma_{12}^2}{2N} + \frac{\mu_{21}}{2} - \frac{\sigma_{21}^2}{2N} - \mu_{22} + \frac{\sigma_{22}^2}{N} \right) \right] \tag{S16}$$

The result is virtually identical to what we found in the diploid case (without imprinting), with the mean and variance of the heterozygotes' reproductive output being replaced by the averages of the means and variances of the two different heterozygotes. That is, we once again recover the standard expression for the change in allele frequency if we define effective fitnesses as  $w_{11} = \mu_{11} - \sigma_{11}^2/N$ ,  $w_{22} = \mu_{22} - \sigma_{22}^2/N$ , and  $w_{12} = (\mu_{12} + \mu_{21})/2 - (\sigma_{12}^2 + \sigma_{21}^2)/(2N)$ .

Often, genomic imprinting involves the transcriptional silencing of one of the two alleles, such that the phenotype of the individual depends only on the maternally inherited (or paternally inherited) allele. For example, if we were considering an imprinted locus with expression only from the maternally inherited allele, we would only need to consider two values of reproductive mean and variance:  $\mu_{1*}$ ,  $\mu_{2*}$ ,  $\sigma_{1*}^2$ , and  $\sigma_{2*}^2$ , where  $*$  indicates either allele. Equation (S16) then reduces to

$$E[\Delta q_1] \approx \frac{q_1q_2}{2} \left( \mu_{1*} - \frac{\sigma_{1*}^2}{N} - \mu_{2*} + \frac{\sigma_{2*}^2}{N} \right), \tag{S17}$$

which is identical to the haploid result, except that the expected change in allele frequency is reduced by a factor of two.

## Two Sexes

We now consider the case where our diploid model has two sexes, in which the same genotype may be associated with different means and variances of reproductive success. To indicate the two sexes, we will include an additional subscript of  $F$  or  $M$  to each of the variables previously introduced. As before, we start

with the mean reproductive success of each type in the population:

$$\begin{aligned}
R_{11F} &= \frac{1}{N_F q_1^2} \sum_{i=1}^{N_F q_1^2} (\mu_{11F} + \alpha_{11Fi}) = \mu_{11F} + \alpha_{11F} \\
R_{12F} &= \frac{1}{N_F q_1 q_2} \sum_{i=1}^{2N_F q_1 q_2} (\mu_{12F} + \alpha_{12Fi}) = \mu_{12F} + \alpha_{12F} \\
R_{21F} &= \frac{1}{N_F q_1 q_2} \sum_{i=1}^{2N_F q_1 q_2} (\mu_{21F} + \alpha_{21Fi}) = \mu_{21F} + \alpha_{21F} \\
R_{22F} &= \frac{1}{N_F q_2^2} \sum_{i=1}^{N_F q_2^2} (\mu_{22F} + \alpha_{22Fi}) = \mu_{22F} + \alpha_{22F} \\
R_{11M} &= \frac{1}{N_M q_1^2} \sum_{i=1}^{N_M q_1^2} (\mu_{11M} + \alpha_{11Mi}) = \mu_{11M} + \alpha_{11M} \\
R_{12M} &= \frac{1}{N_M q_1 q_2} \sum_{i=1}^{2N_M q_1 q_2} (\mu_{12M} + \alpha_{12Mi}) = \mu_{12M} + \alpha_{12M} \\
R_{21M} &= \frac{1}{N_M q_1 q_2} \sum_{i=1}^{2N_M q_1 q_2} (\mu_{21M} + \alpha_{21Mi}) = \mu_{21M} + \alpha_{21M} \\
R_{22M} &= \frac{1}{N_M q_2^2} \sum_{i=1}^{N_M q_2^2} (\mu_{22M} + \alpha_{22Mi}) = \mu_{22M} + \alpha_{22M}.
\end{aligned} \tag{S18}$$

Because the total reproductive output of males and females in the population must be equal, the allele frequency in the next generation will simply be the average of the frequencies of the alleles passed on by males and females. Assuming that mating and sex determination are both independent of the genotype at this locus, this means that we can analyze the two sexes separately. That is,

$$E[\Delta q_1] = \frac{1}{2} \left( \frac{R_{1F}}{\bar{R}_F} - q_1 \right) + \frac{1}{2} \left( \frac{R_{1M}}{\bar{R}_M} - q_1 \right), \tag{S19}$$

where the  $E[\Delta q_1]_*$  terms have the same form as equation (S16). Substituting the appropriate expressions into this equation gives us

$$\begin{aligned}
E[\Delta q_1] &\approx q_1 q_2 \left[ \frac{q_1}{2} \left( \mu_{11F} - \frac{\sigma_{11F}^2}{N_F} - \frac{\mu_{12F}}{2} + \frac{\sigma_{12F}^2}{2N_F} - \frac{\mu_{21F}}{2} + \frac{\sigma_{21F}^2}{2N_F} \right. \right. \\
&\quad \left. \left. + \mu_{11M} - \frac{\sigma_{11M}^2}{N_M} - \frac{\mu_{12M}}{2} + \frac{\sigma_{12M}^2}{2N_M} - \frac{\mu_{21M}}{2} + \frac{\sigma_{21M}^2}{2N_M} \right) \right. \\
&\quad \left. + \frac{q_2}{2} \left( \frac{\mu_{12F}}{2} - \frac{\sigma_{12F}^2}{2N_F} + \frac{\mu_{21F}}{2} - \frac{\sigma_{21F}^2}{2N_F} - \mu_{22F} + \frac{\sigma_{22F}^2}{N_F} \right. \right. \\
&\quad \left. \left. + \frac{\mu_{12M}}{2} - \frac{\sigma_{12M}^2}{2N_M} + \frac{\mu_{21M}}{2} - \frac{\sigma_{21M}^2}{2N_M} - \mu_{22M} + \frac{\sigma_{22M}^2}{N_M} \right) \right].
\end{aligned} \tag{S20}$$

Recall that our earlier analysis involved normalizing the mean and variance by the total expected reproductive output  $E[\bar{R}]$ . In this analysis, that normalization happened separately for males and females. That is, if we want to interpret  $\mu$  and  $\sigma^2$  as the mean and variance of the number of offspring, we would need

to make the following changes:

$$\begin{aligned}
\mu_{*F} &\rightarrow \frac{N_F \mu_{*F}}{N} \\
\mu_{*M} &\rightarrow \frac{N_M \mu_{*M}}{N} \\
\sigma_{*F}^2 &\rightarrow \frac{N_F^2 \sigma_{*F}^2}{N^2} \\
\sigma_{*M}^2 &\rightarrow \frac{N_M^2 \sigma_{*M}^2}{N^2}.
\end{aligned} \tag{S21}$$

We will not make that substitution here, since the separately normalized versions of  $\mu$  and  $\sigma^2$  correspond more closely with our intuitive notions of relative fitness.

Our analysis will focus on the case where the sex ratio is 1:1 ( $N_F = N_M$ ), however, we pause to note a few interesting features of equation (S20). First, the effective mean reproductive success of a genotype is simply the arithmetic mean of the genotype's relative fitness in males and females:  $\mu_* = (\mu_{*F} + \mu_{*M})/2$ . The effective reproductive variance of a genotype, by contrast, is a weighted average that depends more heavily on the reproductive variance in the rarer sex.

$$\sigma_*^2 = N \left( \frac{\sigma_{*F}^2}{N_F} + \frac{\sigma_{*M}^2}{N_M} \right) \tag{S22}$$

Note that this also means that selection will favor bet-hedging phenotypes more in the rarer sex. Given that the benefits of variance reduction are greater in smaller population sizes, this is not surprising. In the case of a 1:1 sex ratio, these effective mean and variance terms can be substituted to recover equation (S16).

## S.4 Two-generation model

The frequency of allele  $A_1$  after two generations follows from equations (2.11) in the main text and is given by

$$q_1' = \frac{q_1(\mu_{1a} + \alpha_{1a})(\mu_{1b} + \alpha_{1b})}{q_1(\mu_{1a} + \alpha_{1a})(\mu_{1b} + \alpha_{1b}) + q_2(\mu_{2a} + \alpha_{2a})(\mu_{2b} + \alpha_{2b})}. \tag{S23}$$

In order to simplify this expression, we introduce the following definitions:

$$\begin{aligned}
\bar{\mu}_{ab} &= q_1\mu_{1a}\mu_{1b} + q_2\mu_{2a}\mu_{2b} \\
\xi_1 &= \mu_{1a}\alpha_{1b} + \mu_{1b}\alpha_{1a} + \alpha_{1a}\alpha_{1b} \\
\xi_2 &= \mu_{2a}\alpha_{2b} + \mu_{2b}\alpha_{2a} + \alpha_{2a}\alpha_{2b}.
\end{aligned} \tag{S24}$$

Substituting this notation into equation (S23) gives us an expression for the change in allele frequency after two generations:

$$\Delta q_1 = q_1 q_2 \frac{\mu_{1a}\mu_{1b} - \mu_{2a}\mu_{2b} + \xi_1 - \xi_2}{\bar{\mu}_{ab} + q_1\xi_1 + q_2\xi_2}. \tag{S25}$$

In this form, we can see that equation (S25) is analogous to equation (1.2) from the main text. The expected reproductive success of alleles  $A_1$  and  $A_2$  is  $\mu_{1a}\mu_{1b}$  and  $\mu_{2a}\mu_{2b}$ , respectively. The terms  $\xi_1$  and  $\xi_2$  are the deviations from those mean values. We scale  $\bar{\mu}_{ab}$  to one as before, and we assume that the difference between the means is small ( $|\mu_{1a}\mu_{1b} - \mu_{2a}\mu_{2b}| \ll 1$ ) and that the total stochastic deviation is small relative to the mean ( $|q_1\xi_1 + q_2\xi_2| \ll 1$ ). We also restrict our analysis to the case where the reproductive success of different individuals is uncorrelated. The expected value of the change in allele frequency is then given approximately by

$$E[\Delta q_1] \approx q_1 q_2 \left( \mu_{1a}\mu_{1b} - \mu_{2a}\mu_{2b} - q_1 E[\xi_1^2] + q_2 E[\xi_2^2] \right). \tag{S26}$$

Substituting the relationships from equation (S24) back in and taking the expectations, as above, yields

$$E[\Delta q_1] \approx q_1 q_2 \left( \mu_{1a}\mu_{1b} - \mu_{2a}\mu_{2b} - q_1 \frac{\mu_{1a}^2 \sigma_{1b}^2}{q_1^2 N} - \frac{\mu_{1b}^2 \sigma_{1a}^2}{N} + q_2 \frac{\mu_{2a}^2 \sigma_{2b}^2}{q_2^2 N} + \frac{\mu_{2b}^2 \sigma_{2a}^2}{N} \right), \tag{S27}$$

where the primes denote the allele frequencies in the intermediate generation, and we have discarded terms of order  $1/N^2$ . Recognizing the fact that  $q'_1 \approx \mu_{1a}q_1$  to the required order, this further reduces to

$$E[\Delta q_1] \approx q_1 q_2 \left( \mu_{1a} \mu_{1b} - \mu_{2a} \mu_{2b} - \frac{\mu_{1a} \sigma_{1b}^2}{N} - \frac{\mu_{1b}^2 \sigma_{1a}^2}{N} + \frac{\mu_{2a} \sigma_{2b}^2}{N} + \frac{\mu_{2b}^2 \sigma_{2a}^2}{N} \right). \quad (\text{S28})$$

## Two-Generation Bet-Hedging at an Imprinted Locus

The logic of the analysis that follows can be grasped intuitively from consideration of equation (2.13) from the main text. If the  $a$  terms in equation (2.13) represent the values in males (averaged across parental origin and genotype), then the  $b$  terms will represent values for paternally inherited alleles (averaged across sex and genotype). Similarly, if  $a$  represents females,  $b$  will represent maternally inherited alleles. Due to the final term in equation (2.13), the benefits of increasing mean reproduction (e.g., at the expense of increased reproductive variance) decline as the reproductive variance in the previous generation increases.

In most species, males have a higher variance of reproductive success than females. That means that in considering the fitness trade-off between increased mean and reduced variance, alleles will receive a greater benefit from reducing reproductive variance when paternally inherited, while alleles will receive greater benefit from increasing the mean when maternally inherited. At an imprinted locus, where alleles exhibit two distinct strategies based on parental origin, natural selection will favor divergent strategies, leading to the type of intragenomic conflict and evolutionary arms race observed in other imprinted systems. At the margin, paternally expressed imprinted genes will favor phenotypic traits that reduce reproductive variance (at the cost of reduced mean reproduction), while maternally expressed imprinted genes will favor traits that increase mean reproduction (at the cost of increased reproductive variance).

We can make this intuitive analysis explicit by first defining the overall reproductive mean and variance for an allele conditional on its being present in males or females. For allele  $A_1$  in females,

$$\begin{aligned} \mu_{1F} &= q_1 \mu_{11F} + \frac{q_2}{2} (\mu_{12F} + \mu_{21F}) \\ \sigma_{1F}^2 &= q_1 \sigma_{11F}^2 + \frac{q_2}{2} (\sigma_{12F}^2 + \sigma_{21F}^2). \end{aligned} \quad (\text{S29})$$

Analogous relationships hold for allele  $A_2$  and for males. We also have similar expressions for the reproductive mean and variance conditional on parental origin. Thus, for allele  $A_1$  when maternally inherited,

$$\begin{aligned} \mu_{1*} &= \frac{q_1}{2} (\mu_{11F} + \mu_{11M}) + \frac{q_2}{2} (\mu_{12F} + \mu_{12M}) = q_1 \mu_{11} + q_2 \mu_{12} \\ \sigma_{1*}^2 &= q_1 (\sigma_{11F}^2 + \sigma_{11M}^2) + q_2 (\sigma_{12F}^2 + \sigma_{12M}^2) = q_1 \sigma_{11}^2 + q_2 \sigma_{12}^2. \end{aligned} \quad (\text{S30})$$

Again, the analogous expressions for  $A_2$  and for paternally inherited alleles are straightforward.

The two-generation effective fitness for allele  $A_1$  is simply the average of equation (2.13) over two sets of alleles. The first is alleles that are present in females in generation  $a$  and are maternally inherited in generation  $b$ . The second is alleles that are present in males in generation  $a$  and are paternally inherited in generation  $b$ :

$$w_1 = \frac{1}{2} \left( \mu_{1F} \mu_{1*} + \mu_{1M} \mu_{*1} - \frac{\mu_{1F} \sigma_{1*}^2}{N} - \frac{\mu_{1M} \sigma_{*1}^2}{N} - \frac{\mu_{1*}^2 \sigma_{1F}^2}{N} - \frac{\mu_{*1}^2 \sigma_{1M}^2}{N} \right). \quad (\text{S31})$$

The term  $w_2$  can be similarly defined (see discussion following supplementary equation (S34) for details), and, with these definitions, the expected change in allele frequency is  $E[\Delta q_1] \approx q_1 q_2 (w_1 - w_2)$ . In order to understand the basis of the intragenomic conflict, we compare this expectation for pairs of alleles  $A_1$  and  $A_2$  in two different contexts: an imprinted locus where only the maternally inherited allele is expressed  $E[\Delta q_1]_m$ , and an imprinted locus where only the paternally inherited allele is expressed  $E[\Delta q_1]_p$ .

For clarity of presentation, our analysis is restricted to the case where the alleles do not have sex-specific effects on mean reproductive success ( $\mu_{1F} = \mu_{1M}$  and  $\mu_{2F} = \mu_{2M}$ ), though it is easy to relax this

assumption. The difference in the expected allele frequency changes is then given by

$$E[\Delta q_1]_m - E[\Delta q_1]_p = \frac{q_1 q_2 (\mu_1^2 - \mu_2^2)}{8N} \left( (1 + 2q_1)(\sigma_{1M}^2 - \sigma_{1F}^2) + (1 + 2q_2)(\sigma_{2M}^2 - \sigma_{2F}^2) \right). \quad (\text{S32})$$

If reproductive variance is greater for males than for females, as is typically the case, then  $E[\Delta q_1]_m - E[\Delta q_1]_p$  will have the same sign as  $\mu_1^2 - \mu_2^2$ . That is, if  $\mu_1 > \mu_2$ , allele  $A_1$  will have a greater advantage over allele  $A_2$  at a maternally expressed imprinted locus than at a paternally expressed one.

The result can perhaps be seen more clearly if we assume that  $\mu_1^2 - \mu_2^2 \approx 2(\mu_1 - \mu_2)$ , which follows if  $\mu_1$  and  $\mu_2$  are both close to 1, and we assume that the difference in male and female reproductive variances is the same for both alleles. We then have

$$E[\Delta q_1]_m - E[\Delta q_1]_p = \frac{q_1 q_2}{N} (\mu_1 - \mu_2) (\sigma_M^2 - \sigma_F^2), \quad (\text{S33})$$

which is our final result discussed below.

## S.5 Two-Generation Model with Imprinting

Here we derive our expression for the expected change in allele frequency  $E[\Delta q_1] = q_1 q_2 (w_1 - w_2)$ , starting from the two-generation effective fitness expressions provided by equation (S31) in the main text and reproduced here:

$$\begin{aligned} w_1 &= \frac{1}{2} \left( \mu_{1F} \mu_{1*} + \mu_{1M} \mu_{*1} - \frac{\mu_{1F} \sigma_{1*}^2}{N} - \frac{\mu_{1M} \sigma_{*1}^2}{N} - \frac{\mu_{1*}^2 \sigma_{1F}^2}{N} - \frac{\mu_{*1}^2 \sigma_{1M}^2}{N} \right) \\ w_2 &= \frac{1}{2} \left( \mu_{2F} \mu_{2*} + \mu_{2M} \mu_{*2} - \frac{\mu_{2F} \sigma_{2*}^2}{N} - \frac{\mu_{2M} \sigma_{*2}^2}{N} - \frac{\mu_{2*}^2 \sigma_{2F}^2}{N} - \frac{\mu_{*2}^2 \sigma_{2M}^2}{N} \right) \end{aligned} \quad (\text{S34})$$

The terms  $\mu_{1F}$ ,  $\mu_{1M}$ ,  $\mu_{2F}$ , and  $\mu_{2M}$  are the mean reproductive success of alleles  $A_1$  and  $A_2$  in females and males, averaged across genotypes. The analogous  $\sigma^2$  terms are the corresponding reproductive variances.

$$\begin{aligned} \mu_{1F} &= q_1 \mu_{11F} + \frac{q_2}{2} (\mu_{12F} + \mu_{21F}) \\ \mu_{2F} &= q_2 \mu_{22F} + \frac{q_1}{2} (\mu_{12F} + \mu_{21F}) \\ \mu_{1M} &= q_1 \mu_{11M} + \frac{q_2}{2} (\mu_{12M} + \mu_{21M}) \\ \mu_{2M} &= q_2 \mu_{22M} + \frac{q_1}{2} (\mu_{12M} + \mu_{21M}) \\ \sigma_{1F}^2 &= q_1 \sigma_{11F}^2 + \frac{q_2}{2} (\sigma_{12F}^2 + \sigma_{21F}^2) \\ \sigma_{2F}^2 &= q_2 \sigma_{22F}^2 + \frac{q_1}{2} (\sigma_{12F}^2 + \sigma_{21F}^2) \\ \sigma_{1M}^2 &= q_1 \sigma_{11M}^2 + \frac{q_2}{2} (\sigma_{12M}^2 + \sigma_{21M}^2) \\ \sigma_{2M}^2 &= q_2 \sigma_{22M}^2 + \frac{q_1}{2} (\sigma_{12M}^2 + \sigma_{21M}^2) \end{aligned} \quad (\text{S35})$$

The term  $\mu_{1*}$  represents the mean reproductive success of maternally inherited  $A_1$  alleles, averaged across genotypes and sexes, while  $\mu_{*1}$  is the mean reproductive success of paternally inherited  $A_1$  alleles. The corresponding values for  $A_2$  are given by  $\mu_{2*}$  and  $\mu_{*2}$ , and again the analogous  $\sigma^2$  terms are the



corresponding reproductive variances.

$$\begin{aligned}
\mu_{1*} &= \frac{q_1}{2} (\mu_{11F} + \mu_{11M}) + \frac{q_2}{2} (\mu_{12F} + \mu_{12M}) = q_1 \mu_{11} + q_2 \mu_{12} \\
\mu_{2*} &= q_2 \mu_{22} + q_1 \mu_{21} \\
\mu_{*1} &= q_1 \mu_{11} + q_2 \mu_{21} \\
\mu_{*2} &= q_2 \mu_{22} + q_1 \mu_{12} \\
\sigma_{1*}^2 &= q_1 (\sigma_{11F}^2 + \sigma_{11M}^2) + q_2 (\sigma_{12F}^2 + \sigma_{12M}^2) = q_1 \sigma_{11}^2 + q_2 \sigma_{12}^2 \\
\sigma_{2*}^2 &= q_2 \sigma_{22}^2 + q_1 \sigma_{21}^2 \\
\sigma_{*1}^2 &= q_1 \sigma_{11}^2 + q_2 \sigma_{21}^2 \\
\sigma_{*2}^2 &= q_2 \sigma_{22}^2 + q_1 \sigma_{12}^2
\end{aligned} \tag{S36}$$

In order to focus our analysis specifically on imprinted gene effects, we will make the simplifying assumption that the alleles do not have sex-specific effects on mean reproductive success (e.g.,  $\mu_{11F} = \mu_{11M} = \mu_{11}$ ).

We now separately consider two cases: an imprinted locus with maternal expression, and an imprinted locus with paternal expression. This allows further simplification. For example, at the maternally expressed locus,  $\mu_{11} = \mu_{12} = \mu_1$ , whereas at the paternally expressed locus,  $\mu_{11} = \mu_{21} = \mu_1$ .

Recalling that our values for  $\mu$  were normalized such that the expected mean reproductive output for the population as a whole (and for males and females separately) is one, for the maternally expressed case our expressions for the reproductive means are

$$\begin{aligned}
\mu_{1F} = \mu_{1M} &= q_1 \mu_1 + \frac{q_2}{2} (\mu_1 + \mu_2) = \frac{1 + \mu_1}{2} \\
\mu_{2F} = \mu_{2M} &= q_2 \mu_2 + \frac{q_1}{2} (\mu_1 + \mu_2) = \frac{1 + \mu_2}{2} \\
\mu_{1*} &= \mu_1 \\
\mu_{2*} &= \mu_2 \\
\mu_{*1} = \mu_{*2} &= q_1 \mu_1 + q_2 \mu_2 = 1
\end{aligned} \tag{S37}$$

This simplifies our effective fitness expressions to

$$\begin{aligned}
w_{1m} &= \frac{1}{2} \left( \frac{1}{2} (1 + \mu_1)^2 - \frac{(1 + \mu_1) \sigma_{1*}^2}{2N} - \frac{(1 + \mu_1) \sigma_{*1}^2}{2N} - \frac{\mu_1^2 \sigma_{1F}^2}{N} - \frac{\sigma_{1M}^2}{N} \right) \\
w_{2m} &= \frac{1}{2} \left( \frac{1}{2} (1 + \mu_2)^2 - \frac{(1 + \mu_2) \sigma_{2*}^2}{2N} - \frac{(1 + \mu_2) \sigma_{*2}^2}{2N} - \frac{\mu_2^2 \sigma_{2F}^2}{N} - \frac{\sigma_{2M}^2}{N} \right)
\end{aligned} \tag{S38}$$

We can also simplify our expressions for reproductive variance. First, we introduce the simplifications associated with assuming that the phenotype depends only on the identity of the maternally inherited allele.

$$\begin{aligned}
\sigma_{1F}^2 &= q_1 \sigma_{1*F}^2 + \frac{q_2}{2} (\sigma_{1*F}^2 + \sigma_{2*F}^2) \\
\sigma_{2F}^2 &= q_2 \sigma_{2*F}^2 + \frac{q_1}{2} (\sigma_{1*F}^2 + \sigma_{2*F}^2) \\
\sigma_{1M}^2 &= q_1 \sigma_{1*M}^2 + \frac{q_2}{2} (\sigma_{1*M}^2 + \sigma_{2*M}^2) \\
\sigma_{2M}^2 &= q_2 \sigma_{2*M}^2 + \frac{q_1}{2} (\sigma_{1*M}^2 + \sigma_{2*M}^2) \\
\sigma_{1*}^2 &= \sigma_{1*F}^2 + \sigma_{1*M}^2 \\
\sigma_{2*}^2 &= \sigma_{2*F}^2 + \sigma_{2*M}^2 \\
\sigma_{*1}^2 = \sigma_{*2}^2 &= q_1 (\sigma_{1*F}^2 + \sigma_{1*M}^2) + q_2 (\sigma_{2*F}^2 + \sigma_{2*M}^2)
\end{aligned} \tag{S39}$$

Next, we reparameterize these equations in terms of the total variance (e.g.,  $\sigma_1^2 = \sigma_{1*F}^2 + \sigma_{1*M}^2$ ) and the difference between male and female variances (e.g.,  $\Delta\sigma_1^2 = \sigma_{1*M}^2 - \sigma_{1*F}^2$ ). The variance expressions then become

$$\begin{aligned}
\sigma_{1F}^2 &= \frac{1+q_1}{2} (\sigma_1^2 - \Delta\sigma_1^2) + \frac{q_2}{2} (\sigma_2^2 - \Delta\sigma_2^2) \\
\sigma_{2F}^2 &= \frac{1+q_2}{2} (\sigma_2^2 - \Delta\sigma_2^2) + \frac{q_1}{2} (\sigma_1^2 - \Delta\sigma_1^2) \\
\sigma_{1M}^2 &= \frac{1+q_1}{2} (\sigma_1^2 + \Delta\sigma_1^2) + \frac{q_2}{2} (\sigma_2^2 + \Delta\sigma_2^2) \\
\sigma_{2M}^2 &= \frac{1+q_2}{2} (\sigma_2^2 + \Delta\sigma_2^2) + \frac{q_1}{2} (\sigma_1^2 + \Delta\sigma_1^2)
\end{aligned} \tag{S40}$$

$$\begin{aligned}
\sigma_{1*}^2 &= \sigma_1^2 \\
\sigma_{2*}^2 &= \sigma_2^2 \\
\sigma_{*1}^2 = \sigma_{*2}^2 &= q_1 \sigma_1^2 + q_2 \sigma_2^2
\end{aligned}$$

Now, substitution into our fitness expressions gives us

$$\begin{aligned}
w_{1m} &= \frac{1}{2} \left( \frac{1}{2} (1 + \mu_1)^2 - \frac{(1 + \mu_1)}{2} \frac{((1 + q_1)\sigma_1^2 + q_2\sigma_2^2)}{N} - \frac{\mu_1^2 ((1 + q_1)(\sigma_1^2 - \Delta\sigma_1^2) + q_2(\sigma_2^2 - \Delta\sigma_2^2))}{2N} \right. \\
&\quad \left. - \frac{(1 + q_1)(\sigma_1^2 + \Delta\sigma_1^2) + q_2(\sigma_2^2 + \Delta\sigma_2^2)}{2N} \right) \\
w_{2m} &= \frac{1}{2} \left( \frac{1}{2} (1 + \mu_2)^2 - \frac{(1 + \mu_2)}{2} \frac{(q_1 \sigma_1^2 + (1 + q_2)\sigma_2^2)}{N} - \frac{\mu_2^2 ((1 + q_2)(\sigma_2^2 - \Delta\sigma_2^2) + q_1(\sigma_1^2 - \Delta\sigma_1^2))}{2N} \right. \\
&\quad \left. - \frac{(1 + q_2)(\sigma_2^2 + \Delta\sigma_2^2) + q_1(\sigma_1^2 + \Delta\sigma_1^2)}{2N} \right)
\end{aligned} \tag{S41}$$

We can contrast these results with the analogous equations for alleles at a paternally expressed imprinted locus. The first terms of the fitness expressions are identical for the two cases. However, the last two terms differ in each case. In the maternally expressed case above, the  $\mu_1^2$  and  $\mu_2^2$  terms are multiplied by the reproductive variances in females. In the paternally expressed case below, these squared mean terms are multiplied by the reproductive variance in males.

$$\begin{aligned}
w_{1p} &= \frac{1}{2} \left( \frac{1}{2} (1 + \mu_1)^2 - \frac{(1 + \mu_1)}{2} \frac{((1 + q_1)\sigma_1^2 + q_2\sigma_2^2)}{N} - \frac{(1 + q_1)(\sigma_1^2 - \Delta\sigma_1^2) + q_2(\sigma_2^2 - \Delta\sigma_2^2)}{2N} \right. \\
&\quad \left. - \frac{\mu_1^2 ((1 + q_1)(\sigma_1^2 + \Delta\sigma_1^2) + q_2(\sigma_2^2 + \Delta\sigma_2^2))}{2N} \right) \\
w_{2p} &= \frac{1}{2} \left( \frac{1}{2} (1 + \mu_2)^2 - \frac{(1 + \mu_2)}{2} \frac{(q_1 \sigma_1^2 + (1 + q_2)\sigma_2^2)}{N} - \frac{(1 + q_2)(\sigma_2^2 - \Delta\sigma_2^2) + q_1(\sigma_1^2 - \Delta\sigma_1^2)}{2N} \right. \\
&\quad \left. - \frac{\mu_2^2 ((1 + q_2)(\sigma_2^2 + \Delta\sigma_2^2) + q_1(\sigma_1^2 + \Delta\sigma_1^2))}{2N} \right)
\end{aligned} \tag{S42}$$

Now, a final substitution will facilitate direct comparison of these results. We set  $\mu_1^2 = 1 + s_2$  and  $\mu_2^2 = 1 - s_2$ . We can then compare the selective advantage of allele  $A_1$  over  $A_2$  at a maternally expressed

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locus with the advantage of a similar allele at a paternally expressed locus. That is, we consider

$$\begin{aligned}
w_{1m} - w_{2m} - (w_{1p} - w_{2p}) = & -\frac{s_2 \left( (1 + q_1)(\sigma_1^2 - \Delta\sigma_1^2) + q_2(\sigma_2^2 - \Delta\sigma_2^2) \right)}{4N} \\
& -\frac{s_2 \left( (1 + q_2)(\sigma_2^2 - \Delta\sigma_2^2) + q_1(\sigma_1^2 - \Delta\sigma_1^2) \right)}{4N} \\
& +\frac{s_2 \left( (1 + q_1)(\sigma_1^2 + \Delta\sigma_1^2) + q_2(\sigma_2^2 + \Delta\sigma_2^2) \right)}{4N} \\
& +\frac{s_2 \left( (1 + q_2)(\sigma_2^2 + \Delta\sigma_2^2) + q_1(\sigma_1^2 + \Delta\sigma_1^2) \right)}{4N}
\end{aligned} \tag{S43}$$

which reduces to

$$w_{1m} - w_{2m} - (w_{1p} - w_{2p}) = \frac{\mu_1^2 - \mu_2^2}{4N} \left( (1 + 2q_1)(\Delta\sigma_1^2) + (1 + 2q_2)(\Delta\sigma_2^2) \right) \tag{S44}$$

If males have a higher variance of reproductive success than females, as is most often the case, the terms  $\Delta\sigma_1^2$  and  $\Delta\sigma_2^2$  will be positive. That means that, in terms of the relative benefits of increased mean and reduced variance, the benefits of increased mean reproductive success are greater for alleles when they are maternally inherited than when they are paternally inherited.