

Derivation of the fixation probability of a mutant

Expected change of mutant frequency. In order to derive the probability of fixation of a mutant, we first evaluate the expected change of mutant frequency over one generation. The frequency of the mutant in a male indexed $i \in \{1, \dots, N_m\}$ is written as $p_{mi} \in \{0, 1/2, 1\}$, and the frequency in a female $j \in \{1, \dots, N_f\}$ is written $p_{fj} \in \{0, 1/2, 1\}$. The indicator variables $\mathbb{1}_{\sigma_i}$ and $\mathbb{1}_{\phi_i}$ respectively take the value one if the paternally and maternally inherited alleles of individual i are mutant, and zero otherwise. Then, the mutant frequencies in male i and in female j are

$$p_{mi} = \frac{\mathbb{1}_{\sigma_i} + \mathbb{1}_{\phi_i}}{2} \quad \text{and} \quad p_{fj} = \frac{\mathbb{1}_{\sigma_j} + \mathbb{1}_{\phi_j}}{2}. \quad (\text{SI.1})$$

We write $\bar{p}_{m,t} = \sum_{i=1}^{N_m} p_{mi,t}/N_m$ and $\bar{p}_{f,t} = \sum_{j=1}^{N_f} p_{fj,t}/N_f$ for the average mutant frequencies in males and females in the population and denote by \mathbf{q}_t the vector collecting the realization of mutant frequencies (the realized values of $\mathbb{1}_{\sigma_i}$ and $\mathbb{1}_{\phi_i}$) in the population at time t .

If the mutant changes male and female phenotypes by δ_m and δ_f and a parent transmits its maternally or paternally inherited gene with equal probability, the expected average male and female mutant frequencies in the next generation is

$$\begin{aligned} E[\bar{p}_{m,t+1} | \mathbf{q}_t] &= \frac{1}{2N_m} \left(\sum_{i=1}^{N_m} p_{mi,t} w_{mi}^m(\delta_m, \delta_f) + \sum_{j=1}^{N_f} p_{fj,t} w_{fj}^m(\delta_m, \delta_f) \right) \\ E[\bar{p}_{f,t+1} | \mathbf{q}_t] &= \frac{1}{2N_f} \left(\sum_{i=1}^{N_m} p_{mi,t} w_{mj}^f(\delta_m, \delta_f) + \sum_{j=1}^{N_f} p_{fj,t} w_{fj}^f(\delta_m, \delta_f) \right), \end{aligned} \quad (\text{SI.2})$$

where $w_{vi}^u(\delta_m, \delta_f)$ is the expected number of adult offspring of sex u of individual i (itself is of sex v) (Price 1970). Eq. (SI.2) extends Rice (2008)'s "selection differential" to a two-sexes populations (his $\text{cov}(\phi, \hat{\Omega})$ term assuming a constant population size).

If selection is weak, it is sufficient to approximate allele frequency change to the first order of phenotypic effect in males and females δ_m and δ_f . The fitness terms w_{vi}^u are approximated as $w_{vi}^u(\delta_m, \delta_f) = w_{vi}^u(\mathbf{0}) + \delta_m(\partial w_{vi}^u(\mathbf{0})/\partial \delta_m) + \delta_f(\partial w_{vi}^u(\mathbf{0})/\partial \delta_f) + O(\delta^2)$, with $\mathbf{0} = (0, 0)$. There are two things to note about the fitness terms and their derivatives. First, in the absence of phenotypic differences, each individual is expected to contribute equally to the next generation, and so $w_{vi}^u(\mathbf{0}) = N_u/N_v$. Second, the partial derivatives of an individual's fitness with respect to phenotypic effect in the other sex is zero $\partial w_{vi}^u(\mathbf{0})/\partial \delta_u = 0$ with $u \neq v$. For instance, when all males are the same ($\delta_m = 0$), changes in female phenotype have no effect on the expected number of adult offspring of a focal male. So substituting for $w_{vi}^u(\delta_m, \delta_f)$ in eq. (SI.2) gives

$$\begin{aligned} E[\bar{p}_{m,t+1} | \mathbf{q}_t] &= \frac{1}{2}(\bar{p}_{m,t} + \bar{p}_{f,t}) + \frac{1}{2N_m} \left(\delta_m \sum_{i=1}^{N_m} p_{mi,t} \frac{\partial w_{mi}^m(\mathbf{0})}{\partial \delta_m} + \delta_f \sum_{j=1}^{N_f} p_{fj,t} \frac{\partial w_{fj}^m(\mathbf{0})}{\partial \delta_f} \right) + O(\delta^2) \\ E[\bar{p}_{f,t+1} | \mathbf{q}_t] &= \frac{1}{2}(\bar{p}_{m,t} + \bar{p}_{f,t}) + \frac{1}{2N_f} \left(\delta_m \sum_{i=1}^{N_m} p_{mi,t} \frac{\partial w_{mj}^f(\mathbf{0})}{\partial \delta_m} + \delta_f \sum_{j=1}^{N_f} p_{fj,t} \frac{\partial w_{fj}^f(\mathbf{0})}{\partial \delta_f} \right) + O(\delta^2). \end{aligned} \quad (\text{SI.3})$$

Another consequence of weak selection is that the fitness derivative of an individual in eq. (SI.3) can be approximated in terms of only three phenotypic values: the phenotype of an individual, the average male phenotype and the average female phenotype. To see this, consider the expected number of female adults produced by male i , w_{mi}^f . This depends on his phenotype z_{mi} , as well as the collection of the phenotypes of all the other males in the population, $\mathbf{z}_{-mi} = \{z_{mk}; k : 1 \rightarrow N_m, k \neq i\}$, as well as those of all the females in the population, $\mathbf{z}_f = \{z_{fj}; j : 1 \rightarrow N_f\}$. Expanded about male population average, excluding male i , $\bar{z}_{-mi} = 1/(N_m - 1) \sum_{k \neq i} z_{mk}$, and female population average $\bar{z}_f = \sum_j z_{fj}/N_f$, w_{mi}^f reads

$$w_{mi}^f(z_{mi}, \mathbf{z}_{-mi}, \mathbf{z}_f) \approx w_{mi}^f(z_{mi}, \bar{z}_{-mi}, \bar{z}_f) + \sum_{k=1, k \neq i}^{N_m} \frac{\partial w_{mi}^f}{\partial z_{mk}} (z_{mk} - \bar{z}_{-mi}) + \sum_{j=1}^{N_f} \frac{\partial w_{mi}^f}{\partial z_{fj}} (z_{fj} - \bar{z}_f), \quad (\text{SI.4})$$

and the remainder is $O(\delta^2)$ because the difference between any two phenotypes of the same sex is of order $O(\delta)$. The effect of changing the phenotype of any female has the same effect on the fitness of male i , so that all $\partial w_{mi}^f / \partial z_{fj}$ are equal, and $\sum_{j=1}^{N_f} (\partial w_{mi}^f / \partial z_{fj}) (z_{fj} - \bar{z}_f) = (\partial w_{mi}^f / \partial z_{fj}) \sum_{j=1}^{N_f} (z_{fj} - \bar{z}_f)$, but by definition, $\sum_{j=1}^{N_f} (z_{fj} - \bar{z}_f) = 0$. A similar argument shows that $\sum_{k=1, k \neq i}^{N_m} (\partial w_{mi}^f / \partial z_{mk}) (z_{mk} - \bar{z}_{-mi}) = 0$. Hence, the female component of fitness of male i , $w_{mi}^f(z_{mi}, \mathbf{z}_{-mi}, \mathbf{z}_f)$, can be approximated by $w_{mi}^f(z_{mi}, \bar{z}_{-mi}, \bar{z}_f)$; that is, as a function of its phenotype, z_{mi} , the average male phenotype excluding the focal, \bar{z}_{-mi} , and the average phenotype of females in the population. However, for computational purposes it may be more convenient to express w_{mi}^f in terms of z_{mi} and the average male phenotype \bar{z}_m . This can be done since $\bar{z}_{-mi} = (N_m \bar{z}_m - z_{mi}) / (N_m - 1)$, so from now on we write the fitness of individual i as $w_{mi}^f(z_{mi}, \bar{z}_m, \bar{z}_f)$, keeping in mind that with this notation $\partial w_{mi}^f(z_{mi}, \bar{z}_{-mi}, \bar{z}_f) / \partial z_{mi} = \partial w_{mi}^f(x, \bar{z}_m, \bar{z}_f) / \partial x + (\partial w_{mi}^f(z_{mi}, \bar{z}_m, \bar{z}_f) / \partial \bar{z}_m) / N_m$. Using the chain rule, the derivatives of fitness with respect to δ_v is $\partial w_{vi}^u / \partial \delta_v = (\partial w_{vi}^u / \partial z_{vi}) (dz_{vi} / d\delta_v) + (\partial w_{vi}^u / \partial \bar{z}_m) (d\bar{z}_m / d\delta_v) + (\partial w_{vi}^u / \partial \bar{z}_f) (d\bar{z}_f / d\delta_v)$. By observing that the average male phenotype is insensitive to changes in female mutant effects ($d\bar{z}_m / d\delta_f = 0$), and that the average female phenotype is insensitive to changes in male mutant effects ($d\bar{z}_f / d\delta_m = 0$), the derivatives of fitness collapse to $\partial w_{vi}^u / \partial \delta_v = (\partial w_{vi}^u / \partial z_{vi}) (dz_{vi} / d\delta_v) + (\partial w_{vi}^u / \partial \bar{z}_v) (d\bar{z}_v / d\delta_v)$. This may be further simplified by noting that since the number of adults of either sex held constant at each generation, any fitness gain made by a focal individual due to a change of phenotype must be compensated by a decrease in fitness by the rest of the population (Rousset 2004, p. 96), i.e., $\partial w_{mi}^u / \partial z_{mi} + \partial w_{mi}^u / \partial \bar{z}_m = 0$ and $\partial w_{fj}^u / \partial z_{fj} + \partial w_{fj}^u / \partial \bar{z}_f = 0$. Thus, we eventually obtain for the derivatives of fitness

$$\frac{\partial w_{vi}^u}{\partial \delta_v} = \frac{\partial w_{vi}^u}{\partial z_{vi}} \left(\frac{dz_{vi}}{d\delta_v} - \frac{d\bar{z}_v}{d\delta_v} \right). \quad (\text{SI.5})$$

Eq. (SI.5) is used to substitute for the derivatives of fitness in eq. (SI.3). To see how, consider the substitution for $\partial w_{mi}^m(\mathbf{0}) / \partial \delta_m$ in

$$\frac{1}{N_m} \sum_{i=1}^{N_m} p_{mi,t} \frac{\partial w_{mi}^m(\mathbf{0})}{\partial \delta_m} = \frac{1}{N_m} \sum_{i=1}^{N_m} p_{mi,t} \frac{\partial w_{mi}^m(\mathbf{0})}{\partial z_{mi}} \left(\frac{dz_{mi}(\mathbf{0})}{d\delta_m} - \frac{d\bar{z}_m(\mathbf{0})}{d\delta_m} \right). \quad (\text{SI.6})$$

At $(\delta_m, \delta_f) = \mathbf{0}$, i.e. where all males are the same, the rate of change of fitness of a male i with respect to its phenotype is the same for all males $\partial w_{mi}^m(\mathbf{0})/\partial z_{mi} = \partial w_{mk}^m(\mathbf{0})/\partial z_{mk}$. Thus, the index i denotes a representative male (or a focal male), rather than a specific one. Then, $\partial w_{mi}^m(\mathbf{0})/\partial z_{mi}$ may be taken out of the sum in eq. (SI.6) and the index dropped for the function w_{mi}^m is dropped, giving

$$\frac{1}{N_m} \sum_{i=1}^{N_m} p_{mi,t} \frac{\partial w_{mi}^m(\mathbf{0})}{\partial \delta_m} = \left(\overline{p_{mi} \frac{dz_{mi}}{d\delta_m}} - \bar{p}_m \frac{d\bar{z}_m}{d\delta_m} \right) \frac{\partial w_m^m(\mathbf{0})}{\partial z_{mi}}, \quad (\text{SI.7})$$

where the overbar with index mi denotes averaging over all males $\overline{x_{mi}} = \sum_{i=1}^{N_m} x_i/N_m$. Using a similar argument for all derivatives of fitness in eq. (SI.3), we obtain

$$\begin{aligned} E[\bar{p}_{m,t+1}|\mathbf{q}_t] &= \frac{1}{2}(\bar{p}_{m,t} + \bar{p}_{f,t}) + \delta_m D_{m,t} \frac{\partial w_m^m(\mathbf{0})}{\partial z_{mi}} + \delta_f \frac{N_f}{N_m} D_{f,t} \frac{\partial w_f^m(\mathbf{0})}{\partial z_{fj}} + O(\delta^2) \\ E[\bar{p}_{f,t+1}|\mathbf{q}_t] &= \frac{1}{2}(\bar{p}_{m,t} + \bar{p}_{f,t}) + \delta_m \frac{N_m}{N_f} D_{m,t} \frac{\partial w_m^f(\mathbf{0})}{\partial z_{mi}} + \delta_f D_{f,t} \frac{\partial w_f^f(\mathbf{0})}{\partial z_{fj}} + O(\delta^2), \end{aligned} \quad (\text{SI.8})$$

where

$$D_{m,t} = \frac{1}{2} \left(\overline{p_{mi} \frac{dz_{mi}}{d\delta_m}} - \bar{p}_m \frac{d\bar{z}_m}{d\delta_m} \right)_t \quad \text{and} \quad D_{f,t} = \frac{1}{2} \left(\overline{p_{fj} \frac{dz_{fj}}{d\delta_f}} - \bar{p}_f \frac{d\bar{z}_f}{d\delta_f} \right)_t, \quad (\text{SI.9})$$

and the overbar with index fj denotes averaging over all females $\overline{x_{fj}} = \sum_{j=1}^{N_f} x_j/N_f$. We have added the subscript t in eq. (SI.9) to make the time dependence of $D_{m,t}$ and $D_{f,t}$ explicit, since they depend on the population genotypic realization at generation t , \mathbf{q}_t .

The expectation of mutant frequencies in males and females from generation t to generation $t+1$ are found by marginalizing eq. (SI.8) over \mathbf{q}_t

$$\begin{aligned} p_{m,t+1} &= E[E[\bar{p}_{m,t+1}|\mathbf{q}_t]] = \sum_{\mathbf{q}_t} E[\bar{p}_{m,t+1}|\mathbf{q}_t] \Pr(\mathbf{q}_t) \\ p_{f,t+1} &= E[E[\bar{p}_{f,t+1}|\mathbf{q}_t]] = \sum_{\mathbf{q}_t} E[\bar{p}_{f,t+1}|\mathbf{q}_t] \Pr(\mathbf{q}_t), \end{aligned} \quad (\text{SI.10})$$

where $\Pr(\mathbf{q}_t)$ is the distribution of allele frequencies at time t . By inspection of eq. (SI.8), we see that only $\bar{p}_{m,t}$, $\bar{p}_{f,t}$, $D_{m,t}$ and $D_{f,t}$ depend on \mathbf{q}_t and thus have to be marginalized over \mathbf{q}_t . Doing so will define the moments of the distribution $\Pr(\mathbf{q}_t)$ required to calculate the expected allele frequency change over one generation. Since $\bar{p}_{m,t}$, $\bar{p}_{f,t}$, $D_{m,t}$ and $D_{f,t}$ are all evaluated in the absence of phenotypic differences $((\delta_m, \delta_f) = \mathbf{0})$, they are marginalized for a neutral process, and the expectation operator is written $E^\circ[\cdot]$. We have $E^\circ[\bar{p}_{m,t}] = p_m$ and $E^\circ[\bar{p}_{f,t}] = p_f$, and evaluate $E^\circ[D_{m,t}]$ and $E^\circ[D_{f,t}]$ below.

We will calculate $E^\circ[\overline{p_{mi}(dz_{mi}/d\delta_m)}]$ and $E^\circ[\overline{p_{fj}(dz_{fj}/d\delta_f)}]$ together, and then $E^\circ[\bar{p}_m(d\bar{z}_m/d\delta_m)]$ and $E^\circ[\bar{p}_f(d\bar{z}_f/d\delta_f)]$, but first, we note that individual phenotype in terms of individual allele frequencies are given by $z_{mi} = z_m + \delta_m(2hp_{mi} + (1-2h)\mathbb{1}_{\sigma_i}\mathbb{1}_{\varnothing_i})$, and $z_{fj} = z_f + \delta_f(2hp_{fj} + (1-2h)\mathbb{1}_{\sigma_j}\mathbb{1}_{\varnothing_j})$. So that average male and female phenotypic values are written as $\bar{z}_m = \sum_i z_{mi}/N_m = z_m + \delta_m(2h\bar{p}_{m,t} + (1-2h)\overline{\mathbb{1}_{\sigma_i}\mathbb{1}_{\varnothing_i}})$ and $\bar{z}_f = \sum_j z_{fj}/N_f = z_f + \delta_f(2h\bar{p}_{f,t} + (1-2h)\overline{\mathbb{1}_{\sigma_j}\mathbb{1}_{\varnothing_j}})$. We then obtain the derivatives with respect to δ of

these averages and the phenotype of male i , which are needed for the population statistics, as

$$\begin{aligned}\frac{dz_{mi}}{d\delta_m} &= 2hp_{mi} + (1 - 2h)\mathbb{1}_{\sigma_i}\mathbb{1}_{\varphi_i} \\ \frac{d\bar{z}_m}{d\delta_m} &= 2h\bar{p}_{m,t} + (1 - 2h)\overline{\mathbb{1}_{\sigma_i}\mathbb{1}_{\varphi_i}} \\ \frac{d\bar{z}_f}{d\delta_f} &= 2h\bar{p}_{f,t} + (1 - 2h)\overline{\mathbb{1}_{\sigma_j}\mathbb{1}_{\varphi_j}}.\end{aligned}\tag{SI.11}$$

Using eq. (SI.1) together with eq. (SI.11), we have

$$\begin{aligned}\mathbb{E}^\circ \left[p_{mi} \frac{dz_{mi}}{d\delta_m} \right]_t &= \mathbb{E}^\circ \left[\frac{\mathbb{1}_{\sigma_i} + \mathbb{1}_{\varphi_i}}{2} \left(h(\mathbb{1}_{\sigma_i} + \mathbb{1}_{\varphi_i}) + (1 - 2h)\mathbb{1}_{\sigma_i}\mathbb{1}_{\varphi_i} \right) \right]_t \\ \mathbb{E}^\circ \left[p_{fj} \frac{dz_{fj}}{d\delta_f} \right]_t &= \mathbb{E}^\circ \left[\frac{\mathbb{1}_{\sigma_j} + \mathbb{1}_{\varphi_j}}{2} \left(h(\mathbb{1}_{\sigma_j} + \mathbb{1}_{\varphi_j}) + (1 - 2h)\mathbb{1}_{\sigma_j}\mathbb{1}_{\varphi_j} \right) \right]_t,\end{aligned}\tag{SI.12}$$

which expanded gives

$$\begin{aligned}\mathbb{E}^\circ \left[p_{mi} \frac{dz_{mi}}{d\delta_m} \right]_t &= \mathbb{E}^\circ \left[\frac{h/2(\mathbb{1}_{\sigma_i} + 2\mathbb{1}_{\sigma_i}\mathbb{1}_{\varphi_i} + \mathbb{1}_{\varphi_i}) + (1 - 2h)\mathbb{1}_{\sigma_i}\mathbb{1}_{\varphi_i}}{2} \right]_t \\ &= \frac{1}{N_m} \mathbb{E}^\circ \left[\sum_{i=1}^{N_m} \frac{h/2(\mathbb{1}_{\sigma_i} + 2\mathbb{1}_{\sigma_i}\mathbb{1}_{\varphi_i} + \mathbb{1}_{\varphi_i}) + (1 - 2h)\mathbb{1}_{\sigma_i}\mathbb{1}_{\varphi_i}}{2} \right]_t \\ &= \mathbb{E}^\circ [h/2(\mathbb{1}_{\sigma_i} + 2\mathbb{1}_{\sigma_i}\mathbb{1}_{\varphi_i} + \mathbb{1}_{\varphi_i}) + (1 - 2h)\mathbb{1}_{\sigma_i}\mathbb{1}_{\varphi_i}]_t,\end{aligned}\tag{SI.13}$$

where we have used that at neutrality, all males are expected to have the same genotypic composition. More succinctly, we write

$$\begin{aligned}\mathbb{E}^\circ \left[p_{mi} \frac{dz_{mi}}{d\delta_m} \right]_t &= h(p_{m,t} + \eta_t) + (1 - 2h)\eta_t \\ \mathbb{E}^\circ \left[p_{fj} \frac{dz_{fj}}{d\delta_f} \right]_t &= h(p_{f,t} + \eta_t) + (1 - 2h)\eta_t,\end{aligned}\tag{SI.14}$$

where $\eta^H = \mathbb{E}^\circ[\mathbb{1}_{\sigma_i}\mathbb{1}_{\varphi_i}]$ is the probability that both the paternal and maternal alleles of an individual are mutants. In the absence of phenotypic differences, this probability is equal for all individuals $\mathbb{E}^\circ[\mathbb{1}_{\sigma_i}\mathbb{1}_{\varphi_i}] = \mathbb{E}^\circ[\mathbb{1}_{\sigma_k}\mathbb{1}_{\varphi_k}]$ for all i and k and irrespective of the sexes of the individuals. To see this, consider the recurrence for η over one generation: $\eta_{t+1} = \mathbb{E}^\circ[\mathbb{1}_{\sigma_i}\mathbb{1}_{\varphi_i}]_{t+1}$. If individual i of generation $t + 1$ has father indexed a and mother indexed c at generation t ,

$$\eta_{t+1} = \frac{1}{4} \mathbb{E}^\circ[(\mathbb{1}_{\sigma_a} + \mathbb{1}_{\varphi_a})(\mathbb{1}_{\sigma_c} + \mathbb{1}_{\varphi_c})]_t,\tag{SI.15}$$

since the paternally inherited mutant of i is equally likely to be the paternally or the maternally inherited mutant of its father a , and the maternally inherited mutant of i is equally likely to be the paternally or the maternally inherited mutant of its mother c . This argument holds whatever the sex of i , so $\eta = \mathbb{E}^\circ[\mathbb{1}_{\sigma_i}\mathbb{1}_{\varphi_i}]$ does not depend on the sex of individual i . A similar argument shows that η is also equal to the probability that a paternally inherited allele and a maternally inherited allele of two different, randomly sampled individuals are mutants, i.e. $\eta = \mathbb{E}^\circ[\mathbb{1}_{\sigma_i}\mathbb{1}_{\varphi_j}] = \mathbb{E}^\circ[\mathbb{1}_{\sigma_j}\mathbb{1}_{\varphi_i}]$ with $i \neq j$.

We now calculate $E^\circ[\bar{p}_m(d\bar{z}_m/d\delta_m)]$ and $E^\circ[\bar{p}_f(d\bar{z}_f/d\delta_f)]$. Using eq. (SI.11) and rearranging to collect the terms that involve the same male i , and those that involve two different males i and k , we have $E^\circ[\bar{p}_m(d\bar{z}_m/d\delta_m)]_t = E^\circ[2h/N_m^2(\sum_i p_{mi}^2 + \sum_{i,k,i \neq k} p_{mi}p_k) + (1-2h)/(N_m^2)(\sum_i p_{mi}\mathbb{1}_{\sigma_i}\mathbb{1}_{\varphi_i} + \sum_{i,k,i \neq k} p_{mi}\mathbb{1}_{\sigma_k}\mathbb{1}_{\varphi_k})]_t$. Letting expectation run through gives $2h/N_m(E^\circ[\overline{p_{mi}^2}]_t + (N_m-1)E^\circ[\overline{p_{mi}p_k}]_t) + (1-2h)/N_m(E^\circ[\overline{p_{mi}\mathbb{1}_{\sigma_i}\mathbb{1}_{\varphi_i}}]_t + (N_m-1)E^\circ[\overline{p_{mi}\mathbb{1}_{\sigma_k}\mathbb{1}_{\varphi_k}}]_t)$ where $i \neq k$. Finally, factoring by $1/N_m$ yields

$$E^\circ \left[\bar{p}_m \frac{d\bar{z}_m}{d\delta_m} \right]_t = \frac{1}{N_m} \left(2h \left(E^\circ[\overline{p_{mi}^2}]_t - E^\circ[\overline{p_{mi}p_k}]_t \right) + (1-2h) \left(E^\circ[\overline{p_{mi}\mathbb{1}_{\sigma_i}\mathbb{1}_{\varphi_i}}]_t - E^\circ[\overline{p_{mi}\mathbb{1}_{\sigma_k}\mathbb{1}_{\varphi_k}}]_t \right) \right) + 2hE^\circ[\overline{p_{mi}p_k}]_t + (1-2h)E^\circ[\overline{p_{mi}\mathbb{1}_{\sigma_k}\mathbb{1}_{\varphi_k}}]_t. \quad (\text{SI.16})$$

Expanding the above in terms of indicator variables for paternally and maternally inherited alleles, we have $E^\circ[p_{mi}^2] = E^\circ[(\mathbb{1}_{\sigma_i} + \mathbb{1}_{\varphi_i} + 2\mathbb{1}_{\sigma_i}\mathbb{1}_{\varphi_i})/4] = (p_m + \eta)/2$, and we write $E^\circ[p_{mi}p_k] = (2\eta + \kappa_m^\sigma + \kappa_m^\varphi)/4$, where $\kappa_m^\sigma = E^\circ[\mathbb{1}_{\sigma_i}\mathbb{1}_{\sigma_k}]$ is the probability that two randomly sampled males $i \neq k$ both inherited the mutant allele from their fathers, and $\kappa_m^\varphi = E^\circ[\mathbb{1}_{\varphi_i}\mathbb{1}_{\varphi_k}]$ is the probability that they inherited the mutant allele from their mothers. Then, $E^\circ[p_{mi}\mathbb{1}_{\sigma_i}\mathbb{1}_{\varphi_i}] = \eta$, and finally $E^\circ[p_{mi}\mathbb{1}_{\sigma_k}\mathbb{1}_{\varphi_k}] = (\rho_m^\sigma + \rho_m^\varphi)/2$, where $\rho_m^\sigma = E^\circ[\mathbb{1}_{\sigma_i}\mathbb{1}_{\sigma_k}\mathbb{1}_{\varphi_k}]$ is the probability that randomly sampled male i has inherited the mutant from its father and that another randomly sampled male k is homozygous for the mutant, and $\rho_m^\varphi = E^\circ[\mathbb{1}_{\varphi_i}\mathbb{1}_{\sigma_k}\mathbb{1}_{\varphi_k}]$ is the probability that randomly sampled male i has inherited the mutant from its mother and that another randomly sampled male k is homozygous for the mutant. After using the similar argument for $E^\circ[p_f d\bar{z}_f]$, we find that at generation t

$$E^\circ \left[\bar{p}_m \frac{d\bar{z}_m}{d\delta_m} \right]_t = \frac{1}{N_m} \left\{ h \left(p_{m,t} - \frac{\kappa_t^\sigma + \kappa_t^\varphi}{2} \right) + (1-2h) \left(\eta_t - \frac{\rho_t^\sigma + \rho_t^\varphi}{2} \right) \right\} + h \left(\eta_t + \frac{\kappa_t^\sigma + \kappa_t^\varphi}{2} \right) + (1-2h) \left(\frac{\rho_t^\sigma + \rho_t^\varphi}{2} \right), \quad (\text{SI.17})$$

$$E^\circ \left[\bar{p}_f \frac{d\bar{z}_f}{d\delta_f} \right]_t = \frac{1}{N_f} \left\{ h \left(p_{f,t} - \frac{\kappa_t^\sigma + \kappa_t^\varphi}{2} \right) + (1-2h) \left(\eta_t - \frac{\rho_t^\sigma + \rho_t^\varphi}{2} \right) \right\} + h \left(\eta_t + \frac{\kappa_t^\sigma + \kappa_t^\varphi}{2} \right) + (1-2h) \left(\frac{\rho_t^\sigma + \rho_t^\varphi}{2} \right),$$

where for two randomly sampled females $j \neq l$, $\kappa_f^\sigma = E^\circ[\mathbb{1}_{\sigma_j}\mathbb{1}_{\sigma_l}]$, $\kappa_f^\varphi = E^\circ[\mathbb{1}_{\varphi_j}\mathbb{1}_{\varphi_l}]$, $\rho_f^\sigma = E^\circ[\mathbb{1}_{\sigma_j}\mathbb{1}_{\sigma_l}\mathbb{1}_{\varphi_l}]$ and $\rho_f^\varphi = E^\circ[\mathbb{1}_{\varphi_j}\mathbb{1}_{\sigma_l}\mathbb{1}_{\varphi_l}]$.

Substituting eqs. (SI.14) and (SI.17) into eq. (SI.8), we find that the unconditional expected allele frequencies in the males and females of the next generation are given by

$$p_{m,t+1} = \frac{1}{2}(p_{m,t} + p_{f,t}) + \delta_m K_{m,t} \frac{\partial w_m^m(\mathbf{0})}{\partial z_{mi}} + \delta_f \frac{N_f}{N_m} K_{f,t} \frac{\partial w_f^m(\mathbf{0})}{\partial z_{fj}} \quad (\text{SI.18})$$

$$p_{f,t+1} = \frac{1}{2}(p_{m,t} + p_{f,t}) + \delta_m \frac{N_m}{N_f} K_{m,t} \frac{\partial w_m^f(\mathbf{0})}{\partial z_{mi}} + \delta_f K_{f,t} \frac{\partial w_f^f(\mathbf{0})}{\partial z_{fj}}.$$

where

$$K_{u,t} = \frac{1}{2} \left(1 - \frac{1}{N_u} \right) \left[h \left(p_{u,t} - \frac{\kappa_{u,t}^\sigma + \kappa_{u,t}^\varphi}{2} \right) + (1-2h) \left(\eta_t - \frac{\rho_{u,t}^\sigma + \rho_{u,t}^\varphi}{2} \right) \right], \quad (\text{SI.19})$$

for $u \in \{m, f\}$. The latter can be interpreted as the neutral expectation of the covariance between genotype and phenotype at generation t in an individual of sex u . Indeed, from eqs. (SI.6) and (SI.10), we have that K_u is also equal to

$$K_{u,t} = \frac{1}{2} E^\circ \left[\frac{1}{N_u} \sum_i^{N_u} p_{ui,t} \left(\frac{dz_{ui}(\mathbf{0})}{d\delta_u} - \frac{d\bar{z}_u(\mathbf{0})}{d\delta_u} \right) \right], \quad (\text{SI.20})$$

and since $z_{ui} = z_u + \delta_u(2hp_{ui} + (1 - 2h)\mathbb{1}_{\sigma_i}\mathbb{1}_{\varphi_i})$, this may be written as

$$\begin{aligned} K_{u,t} &= \frac{1}{2} \frac{1}{\delta_u} E^\circ \left[\frac{1}{N_u} \sum_i^{N_u} p_{ui,t} (z_{ui} - \bar{z}_u) \right] \\ &= \frac{1}{2} \frac{1}{\delta_u} E^\circ \left[\frac{1}{N_u} \sum_i^{N_u} (p_{ui,t} - \bar{p}_{ui,t}) (z_{ui} - \bar{z}_u) \right]. \end{aligned} \quad (\text{SI.21})$$

Therefore, $K_{u,t}$ is proportional to the expected covariance $E^\circ [C[p_{ui,t}, z_{ui}]]$ at generation t between individual genotype and phenotype in sex u , when mutant frequencies $p_{ui,t}$ evolve neutrally.

Closing the recursion. Eq. (SI.18) gives the change of p_m and p_f over one generation, which depends on higher moments of the distribution of the mutant in the population (η_t , $\kappa_{u,t}^{\sigma}$, $\kappa_{u,t}^{\varphi}$, $\rho_{u,t}^{\sigma}$, and $\rho_{u,t}^{\varphi}$). These latter also change from one generation to the next, and in order to evaluate the change of $p_{m,t}$ and $p_{f,t}$ over more than one generation, we need to characterize these recursions. Since they are evaluated at $(\delta_m, \delta_f) = \mathbf{0}$ in eq. (SI.18), it is sufficient to evaluate the recursions for η_t , $\kappa_{u,t}^{\sigma}$, $\kappa_{u,t}^{\varphi}$, $\rho_{u,t}^{\sigma}$, and $\rho_{u,t}^{\varphi}$ at neutrality, where they are only affected by genetic drift. We give these recursions below using standard population genetic methods (Karlin 1968, for example).

The probability that a gene sampled in an individual is mutant does not depend on the sex of the individual as it comes with equal probability from its father or its mother

$$p_{m,t+1} = p_{f,t+1} = \frac{1}{2} (E^\circ [\mathbb{1}_{\sigma_i} + \mathbb{1}_{\sigma_i}]_t) = \frac{1}{2} (p_{m,t} + p_{f,t}). \quad (\text{SI.22})$$

The probability that the paternally and the maternally inherited allele of individual i at time $t+1$ are both mutant, η_{t+1} , is given in terms of neutral moments of gene frequency at generation t in eq. (SI.15) which, if expanded, gives

$$\eta_{t+1} = \frac{1}{4} (2\eta_t + \kappa_{c,t}^{\sigma} + \kappa_{c,t}^{\varphi}). \quad (\text{SI.23})$$

where for a male i and a female j , $\kappa_c^{\sigma} = E^\circ [\mathbb{1}_{\sigma_i}\mathbb{1}_{\sigma_j}]$, and $\kappa_c^{\varphi} = E^\circ [\mathbb{1}_{\varphi_i}\mathbb{1}_{\varphi_j}]$.

The probability that two paternally inherited alleles randomly sampled in two different males are both mutants at generation $t+1$, $\kappa_{m,t+1}^{\sigma}$, depends on whether the two males have the same father, which occurs with a probability denoted Θ_m^{σ} or not (which occurs with probability $1 - \Theta_m^{\sigma}$). These probabilities are referred to as probabilities of sibships. If the two males have the same father, which we index a , then their paternal alleles can be either both copies of the paternal gene of a (with probability $1/4$), both copies of the maternal gene of a (with probability

1/4), or one is a paternal copy and one is a maternal copy (with probability 1/2). So, if two males have the same father, their two paternally sampled genes are mutants with probability $(1/4)\mathbb{E}^\circ[(\mathbb{1}_{\sigma_a} + \mathbb{1}_{\varphi_a})^2]_t$. If they have different fathers, indexed a and b , then the paternal copy of the first male may be the paternal or maternal copy of a (each with probability 1/2), and the paternal copy of the second male may be the paternal or maternal copy of b (also each with probability 1/2). In this case, the paternal alleles of the two individuals are both mutants with probability $(1/4)\mathbb{E}^\circ[(\mathbb{1}_{\sigma_a} + \mathbb{1}_{\varphi_a})(\mathbb{1}_{\sigma_b} + \mathbb{1}_{\varphi_b})]_t$. Combining these two cases, the probability that two randomly sampled paternal alleles of different males at generation $t + 1$ are mutants is $\kappa_{m,t+1}^{\sigma} = \Theta_m^{\sigma}(1/4)\mathbb{E}^\circ[(\mathbb{1}_{\sigma_a} + \mathbb{1}_{\varphi_a})^2]_t + (1 - \Theta_m^{\sigma})(1/4)\mathbb{E}^\circ[(\mathbb{1}_{\sigma_a} + \mathbb{1}_{\varphi_a})(\mathbb{1}_{\sigma_b} + \mathbb{1}_{\varphi_b})]_t$ which, after letting expectation $\mathbb{E}^\circ[\cdot]$ run through and using previous definitions, gives $\kappa_{m,t+1}^{\sigma} = \Theta_m^{\sigma}(2\eta_t + p_{m,t} + p_{f,t})/4 + (1 - \Theta_m^{\sigma})(2\eta_t + \kappa_{m,t}^{\sigma} + \kappa_{m,t}^{\varphi})/4$. In fact, we find more generally that the probabilities that the paternal alleles of two males ($x = m$), or of two females ($x = f$), or of a male and female ($x = c$) are mutants at generation $t + 1$ are given by

$$\kappa_{x,t+1}^m = \frac{\Theta_x^{\sigma}}{4}(2\eta_t + p_{m,t} + p_{f,t}) + \frac{1 - \Theta_x^{\sigma}}{4}(2\eta_t + \kappa_{m,t}^{\sigma} + \kappa_{m,t}^{\varphi}) \quad (\text{SI.24})$$

where Θ_f^{σ} is the probability that two females have the same father and, Θ_c^{σ} is the probability that a male and a female have the same father.

Using a similar argument, we find that the probabilities that the maternal alleles of two males ($x = m$), or of two females ($x = f$), or of a male and female ($x = c$) are mutants at generation $t + 1$ are given by

$$\kappa_{x,t+1}^{\varphi} = \frac{\Theta_x^{\varphi}}{4}(2\eta_t + p_{m,t} + p_{f,t}) + \frac{1 - \Theta_x^{\varphi}}{4}(2\eta_t + \kappa_{f,t}^{\sigma} + \kappa_{f,t}^{\varphi}), \quad (\text{SI.25})$$

where Θ_x^{φ} is the probability that two individuals, whose sexes are given by x , have the same mother.

The probability $\rho_{m,t+1}^{\sigma} = \mathbb{E}^\circ[\mathbb{1}_{\sigma_i} \mathbb{1}_{\sigma_k} \mathbb{1}_{\varphi_c}]_{t+1}$ that two (different) paternally inherited alleles and one maternally inherited allele at generation $t + 1$ are mutants depends on whether the males from which the paternal alleles are sampled (males i and k here) have the same father (indexed a) or different fathers (a and b). Using a similar argument as in the preceding section, and indexing by c the mother of the male who holds the maternal allele, we have $\rho_{m,t+1}^{\sigma} = \Theta_m^{\sigma}(1/8)\mathbb{E}^\circ[(\mathbb{1}_{\sigma_a} + \mathbb{1}_{\varphi_a})^2(\mathbb{1}_{\sigma_c} + \mathbb{1}_{\varphi_c})]_t + (1 - \Theta_m^{\sigma})(1/8)\mathbb{E}^\circ[(\mathbb{1}_{\sigma_a} + \mathbb{1}_{\varphi_a})(\mathbb{1}_{\sigma_b} + \mathbb{1}_{\varphi_b})(\mathbb{1}_{\sigma_c} + \mathbb{1}_{\varphi_c})]_t$. Then, expanding and letting expectation run through, we have: $\rho_{m,t+1}^{\sigma} = \Theta_m^{\sigma} \left(2\eta_t + \kappa_{c,t}^{\sigma} + \kappa_{c,t}^{\varphi} + 2\rho_{c,t}^{\sigma} + 2\rho_{c,t}^{\varphi} \right) / 8 + (1 - \Theta_m^{\sigma}) \left(\varsigma_{2m,t}^{\sigma} + \varsigma_{2m,t}^{\varphi} + 2\rho_{c,t}^{\sigma} + 2\rho_{c,t}^{\varphi} + \rho_{m,t}^{\sigma} + \rho_{m,t}^{\varphi} \right) / 8$, where $\varsigma_{2m,t}^{\sigma} = \mathbb{E}^\circ[\mathbb{1}_{\sigma_a} \mathbb{1}_{\sigma_b} \mathbb{1}_{\sigma_c}]_t$ and $\varsigma_{2m,t}^{\varphi} = \mathbb{E}^\circ[\mathbb{1}_{\varphi_a} \mathbb{1}_{\varphi_b} \mathbb{1}_{\varphi_c}]_t$ are the probabilities that the paternal and maternal alleles, respectively, of two randomly sampled (without replacement) males a and b and a female c at generation t are all mutants. We find in general that for $x \in \{m, f, c\}$

$$\begin{aligned} \rho_{x,t+1}^{\sigma} = & \frac{\Theta_x^{\sigma}}{8} \left(2\eta_t + \kappa_{c,t}^{\sigma} + \kappa_{c,t}^{\varphi} + 2\rho_{c,t}^{\sigma} + 2\rho_{c,t}^{\varphi} \right) \\ & + \frac{1 - \Theta_x^{\sigma}}{8} \left(\varsigma_{2m,t}^{\sigma} + \varsigma_{2m,t}^{\varphi} + 2\rho_{c,t}^{\sigma} + 2\rho_{c,t}^{\varphi} + \rho_{m,t}^{\sigma} + \rho_{m,t}^{\varphi} \right) \end{aligned} \quad (\text{SI.26})$$

Similarly, the probability that two (different) maternally inherited alleles and one paternally inherited allele from two individuals are mutants at generation $t + 1$, $\rho_{x,t+1}^{\circ} = E^{\circ}[\mathbb{1}_{\circ i} \mathbb{1}_{\circ j} \mathbb{1}_{\sigma k}]_{t+1}$, depends on whether individuals i and j from which maternal genes are sampled have the same mother (indexed c) or different mothers (c and d), $\rho_{t+1}^{\circ} = \Theta_x^{\circ}(1/8)E^{\circ}[(\mathbb{1}_{\sigma c} + \mathbb{1}_{\circ c})^2(\mathbb{1}_{\sigma a} + \mathbb{1}_{\circ a})]_t + (1 - \Theta_x^{\circ})(1/8)E^{\circ}[(\mathbb{1}_{\sigma c} + \mathbb{1}_{\circ c})(\mathbb{1}_{\sigma d} + \mathbb{1}_{\circ d})(\mathbb{1}_{\sigma a} + \mathbb{1}_{\circ a})]_t$, where a is the father of the individual whose paternal gene is sampled. Then for $x \in \{m, f, c\}$

$$\begin{aligned} \rho_{x,t+1}^{\circ} = & \frac{\Theta_x^{\sigma}}{8} \left(2\eta_t + \kappa_{c,t}^{\sigma} + \kappa_{c,t}^{\circ} + 2\rho_{c,t}^{\sigma} + 2\rho_{c,t}^{\circ} \right) \\ & + \frac{1 - \Theta_x^{\sigma}}{8} \left(\varsigma_{2m,t}^{\sigma} + \varsigma_{2m,t}^{\circ} + 2\rho_{c,t}^{\sigma} + 2\rho_{c,t}^{\circ} + \rho_{f,t}^{\sigma} + \rho_{f,t}^{\circ} \right) \end{aligned} \quad (\text{SI.27})$$

where $\varsigma_{2f,t}^{\sigma} = E^{\circ}[\mathbb{1}_{\sigma a} \mathbb{1}_{\sigma c} \mathbb{1}_{\sigma d}]_t$ and $\varsigma_{2f,t}^{\circ} = E^{\circ}[\mathbb{1}_{\circ a} \mathbb{1}_{\circ c} \mathbb{1}_{\circ d}]_t$ are the probabilities that the paternal and maternal alleles, respectively, of a male a and of two different females c and d at generation t are all mutants.

The probability that three alleles sampled from different individuals are mutants depends on the probabilities of sibship of three individuals. In order to consider the iteration of the probability ς_x^{σ} , i.e. that three randomly chosen paternally inherited genes are mutants, we need to separate the cases where all three individuals are males (subscript $x = 3m$), all three are females ($x = 3f$), two are males and one is female ($x = 2m$), or two are females and one is male ($x = 2f$). The probabilities that three paternal alleles are mutants then depend on whether all three individuals have the same father, which occurs with a probability we write as $\Xi 3_x^{\sigma}$, whether only two have a same father (with probability $\Xi 2_x^{\sigma}$), or if none of the three have the same father (with probability $1 - \Xi 3_x^{\sigma} - \Xi 2_x^{\sigma}$). If they all have the same father (indexed a), then they are all mutants if they have inherited the mutant gene from the maternal or paternal locus from a . And similar arguments apply for the case when only two have the same father (indexed a , and the other father is indexed b) or if they have three different fathers (indexed a , b and c) to give $\varsigma_{x,t+1}^{\sigma} = \Xi 3_x^{\sigma} E^{\circ}[(\mathbb{1}_{\sigma a} + \mathbb{1}_{\circ a})^3]_t/8 + \Xi 2_x^{\sigma} E^{\circ}[(\mathbb{1}_{\sigma a} + \mathbb{1}_{\circ a})^2(\mathbb{1}_{\sigma b} + \mathbb{1}_{\circ b})]_t/8 + (1 - \Xi 3_x^{\sigma} - \Xi 2_x^{\sigma}) E^{\circ}[(\mathbb{1}_{\sigma a} + \mathbb{1}_{\circ a})(\mathbb{1}_{\sigma b} + \mathbb{1}_{\circ b})(\mathbb{1}_{\sigma c} + \mathbb{1}_{\circ c})]_t/8$, which, expanding and letting expectation run through, results in

$$\begin{aligned} \varsigma_{x,t+1}^{\sigma} = & \frac{\Xi 3_x^{\sigma}}{8} (p_{m,t} + p_{f,t} + 6\eta_t) + \frac{\Xi 2_x^{\sigma}}{8} (2\eta_t + \kappa_{m,t}^{\sigma} + \kappa_{m,t}^{\circ} + 2\rho_{m,t}^{\sigma} + 2\rho_{m,t}^{\circ}) \\ & + \frac{1 - \Xi 3_x^{\sigma} - \Xi 2_x^{\sigma}}{8} (\varsigma_{3m,t}^{\sigma} + \varsigma_{3m,t}^{\circ} + 3\rho_{m,t}^{\sigma} + 3\rho_{m,t}^{\circ}). \end{aligned} \quad (\text{SI.28})$$

Similarly, the probability that three randomly chosen maternally inherited genes ς_x° are mutants can be expressed in terms of the probabilities that the individuals have the same mother,

$$\begin{aligned} \varsigma_{x,t+1}^{\circ} = & \frac{\Xi 3_x^{\circ}}{8} (p_{m,t} + p_{f,t} + 6\eta_t) + \frac{\Xi 2_x^{\circ}}{8} (2\eta_t + \kappa_{f,t}^{\sigma} + \kappa_{f,t}^{\circ} + 2\rho_{f,t}^{\sigma} + 2\rho_{f,t}^{\circ}) \\ & + \frac{1 - \Xi 3_x^{\circ} - \Xi 2_x^{\circ}}{8} (\varsigma_{3f,t}^{\sigma} + \varsigma_{3f,t}^{\circ} + 3\rho_{f,t}^{\sigma} + 3\rho_{f,t}^{\circ}) \end{aligned} \quad (\text{SI.29})$$

where $\Xi 3_x^{\circ}$ is the probability that the three holders (whose sexes are given by $x \in \{3m, 3f, 2m, 2f\}$) have the

same mother, and $\Xi 2_x^\circ$ is the probability that out of the three individuals, two have the same mother. The moments $\varsigma_{x,t+1}^\sigma$ and $\varsigma_{x,t+1}^\circ$ ($x \in \{3m, 3f\}$) also satisfy the recurrences given by eqs. (SI.28)(SI.29), and complete the necessary moments to iterate eq. (SI.18).

Probability of fixation of an autosomal mutant. We proceed to calculate the probability of fixation of the mutant by iterating its expected change over many generations. Eqs. (SI.22) - (SI.29) define the changes in the moments of the population genotypic distribution of a neutral mutant. Since eqs. (SI.22) - (SI.29) are all linear in the relevant moments, we may express the set of recurrences as a matrix operation: $\mathbf{p}_{t+1} = \mathbf{A}^\circ \mathbf{p}_t$, where \mathbf{p}_t is a 23×1 vector which collects the necessary moments of $\Pr(\mathbf{q}_t)$ ($p_m, p_f, \eta, \kappa_x^\sigma, \kappa_x^\circ, \rho_x^\sigma, \rho_x^\circ, \varsigma_y^\sigma, \varsigma_y^\circ$) for $x \in \{m, c, f\}$, $y \in \{3m, 3f, 2m, 2f\}$, and \mathbf{A}° is a 23×23 matrix defined by eqs. (SI.22) - (SI.29).

Eq. (SI.18) adds the effects of selection to the expected mutant frequency change. Since it is also linear in $p_m, p_f, \eta, \kappa_x^\sigma, \kappa_x^\circ, \rho_x^\sigma$, and ρ_x° , it may also be represented as a matrix operation, giving

$$\mathbf{p}_{t+1} = \mathbf{A} \mathbf{p}_t \quad \text{with} \quad \mathbf{A} = \mathbf{A}^\circ + \delta_m \dot{\mathbf{A}}_m + \delta_f \dot{\mathbf{A}}_f + O(\delta^2), \quad (\text{SI.30})$$

where the 23×23 matrices $\dot{\mathbf{A}}_m$ and $\dot{\mathbf{A}}_f$ describes the first order perturbation of average frequency change due to mutant effect in males and females respectively. Eq. (SI.30) fully characterizes the expected frequency change of a mutant in a sexually dimorphic population at any generation i.e., the model is dynamically sufficient.

Explicit expression for these large matrices are omitted from this paper, but they can be found straightforwardly from eqs. (SI.22) - (SI.29) for \mathbf{A}° and from eq. (SI.18) for $\dot{\mathbf{A}}_m$ and $\dot{\mathbf{A}}_f$. Their entries will of course depend on the order chosen for the entries of \mathbf{p}_t . We will assume here that the first 15 entries of \mathbf{p}_t are $\mathbf{p}_t = (p_m, p_f, \eta, \kappa_m^\sigma, \kappa_c^\sigma, \kappa_f^\sigma, \kappa_m^\circ, \kappa_c^\circ, \kappa_f^\circ, \rho_m^\sigma, \rho_c^\sigma, \rho_f^\sigma, \rho_m^\circ, \rho_c^\circ, \rho_f^\circ, \dots)^T$.

We derive the expression for the fixation probability π of the mutant by estimating the asymptotic sum of expected allele-frequency change of the allele in males and females (Leturque and Rousset 2002; Rousset 2004; Lessard and Ladret 2007; Lehmann and Rousset 2009). The fixation probability of the mutant π_m in males, and π_f in females is the asymptotic average frequency of the mutant in each sex

$$\pi_m = \lim_{t \rightarrow \infty} p_{m,t}, \quad \pi_f = \lim_{t \rightarrow \infty} p_{f,t}. \quad (\text{SI.31})$$

Because the mutant allele eventually is either eliminated or fixated in the population, the fixation probability in males and females is the same $\pi_m = \pi_f = \pi$. The fixation probabilities in males and females could be obtained from the asymptotic vector $\lim_{t \rightarrow \infty} \mathbf{A}^t \mathbf{p}_0$, but this is difficult as it requires the calculation of \mathbf{A} 's eigenvectors. We rely on an alternative scheme to obtain π . To that aim, it is convenient to express the fixation probability of the mutant as the average

$$\pi = \alpha \pi_m + (1 - \alpha) \pi_f, \quad (\text{SI.32})$$

where the weight α is chosen such that the expected frequency change of a neutral mutant in any generation t is

zero: $\alpha E[\Delta p_{m,t}] + (1 - \alpha) E[\Delta p_{f,t}] = 0$. In this case, $\alpha = 1/2$ for a diploid, autosomal genetic system. Together, eqs. (SI.31) & (SI.32) imply that π is the average sum of gene frequency change in males and females, from the appearance to the eventual fixation or loss of the mutant

$$\pi = \alpha p_{m,0} + (1 - \alpha) p_{f,0} + \sum_{t=0}^{\infty} \left(\alpha E[\Delta p_{m,t}] + (1 - \alpha) E[\Delta p_{f,t}] \right). \quad (\text{SI.33})$$

The probability of fixation of a mutant with initial frequencies $p_{m,0}$ in males and $p_{f,0}$ females is approximated to the first order of δ : $\pi = \alpha p_{m,0} + (1 - \alpha) p_{f,0} + \alpha \delta_m (\partial \pi(\mathbf{0}) / \partial \delta_m) + (1 - \alpha) \delta_f (\partial \pi(\mathbf{0}) / \partial \delta_f) + O(\delta^2)$. We begin by considering the first order effects of male phenotype on π . Using eq. (SI.33), it is $\partial \pi(\mathbf{0}) / \partial \delta_m = (\partial / \partial \delta_m) \sum_{t=0}^{\infty} (\alpha E[\Delta p_{m,t}] + (1 - \alpha) E[\Delta p_{f,t}])_{\delta_m = \delta_f = 0}$. In matrix notation, this is $\partial \pi(\mathbf{0}) / \partial \delta_m = \alpha \cdot \sum_{t=0}^{\infty} (\partial / \partial \delta_m) (\mathbf{p}_{t+1} - \mathbf{p}_t)_{\delta_m = \delta_f = 0}$ where $\mathbf{p} = p_m, p_f, \dots$ and $\alpha = (\alpha, 1 - \alpha, 0, \dots, 0)$ is such that when dot multiplied with \mathbf{p}_t , it collects and sums $p_{m,t}$ and $p_{f,t}$ weighted by the reproductive values. Then, using eqs. (SI.30), we have $\partial (\mathbf{p}_{t+1} - \mathbf{p}_t) / \partial \delta_m = \dot{\mathbf{A}}_m \mathbf{p}_t$. So the male perturbation of the probability of fixation may be written as

$$\frac{\partial \pi(\mathbf{0})}{\partial \delta_m} = \alpha \cdot \sum_{t=0}^{\infty} \dot{\mathbf{A}}_m \mathbf{p}_t \Big|_{\delta_m = \delta_f = 0}. \quad (\text{SI.34})$$

The sum $\sum_{t=0}^{\infty} \mathbf{p}_t|_{\delta_m = \delta_f = 0}$, which we write as $\sum_{t=0}^{\infty} \mathbf{p}_t^\circ$ where $\mathbf{p}_{t+1}^\circ = \mathbf{A}^\circ \mathbf{p}_t^\circ$, does not converge as \mathbf{A}° is not regular. This means $\dot{\mathbf{A}}$ cannot be factored out of the sum in eq. (SI.34). To circumvent this problem, we construct an iteration around a centred variable using the zero row-sum property of matrix $\dot{\mathbf{A}}_m$ (Lehmann and Rousset 2009). To that aim, we define a vector \mathbf{q}_t° and a matrix \mathbf{Q}° such that (i) $\sum_{t=0}^{\infty} \dot{\mathbf{A}}_m \mathbf{p}_t^\circ = \sum_{t=0}^{\infty} \dot{\mathbf{A}}_m (\mathbf{p}_t^\circ - \mathbf{q}_t^\circ)$, (ii) $\mathbf{p}_{t+1}^\circ - \mathbf{q}_{t+1}^\circ = (\mathbf{A}^\circ - \mathbf{Q}^\circ)(\mathbf{p}_t^\circ - \mathbf{q}_t^\circ)$, and (iii) $\lim_{t \rightarrow \infty} (\mathbf{p}_t^\circ - \mathbf{q}_t^\circ) = 0$. The choice of \mathbf{q}_t° with all vector elements being equal to $\alpha p_{f,t} + (1 - \alpha) p_{m,t}$, which acts as a reference variable, and $\mathbf{Q}^\circ = (q_{ij})$ with all elements of column 1 being equal to α , all elements of column 2 being equal to $1 - \alpha$, and zero otherwise satisfies all three conditions. In effect, this choice of the vector \mathbf{q}_t° centers the iteration around the mutant frequency averaged across the sexes according to their reproductive class (this average is the reference variable), while \mathbf{Q}° provides the iteration of the reference variable.

Using properties (i)-(iii) in the preceding paragraph, we can now factorize $\sum_{t=0}^{\infty} \dot{\mathbf{A}}_m \mathbf{p}_t = \dot{\mathbf{A}}_m \sum_{t=0}^{\infty} (\mathbf{p}_t^\circ - \mathbf{q}_t^\circ) = \dot{\mathbf{A}}_m \sum_{t=0}^{\infty} (\mathbf{A}^\circ - \mathbf{Q}^\circ)^t (\mathbf{p}_0 - \mathbf{q}_0^\circ)$. With all eigenvalues of $(\mathbf{A}^\circ - \mathbf{Q}^\circ)$ being less than 1 in absolute value (Lehmann and Rousset 2009, p. 47), the sum $\mathbf{d}^\circ = \sum_{t=0}^{\infty} (\mathbf{A}^\circ - \mathbf{Q}^\circ)^t (\mathbf{p}_0 - \mathbf{q}_0^\circ)$ can be evaluated as $[\mathbf{I} - \mathbf{A}^\circ + \mathbf{Q}^\circ]^{-1}$, where \mathbf{I} is the identity matrix, so we have

$$\frac{\partial \pi(\mathbf{0})}{\partial \delta_m} = \alpha \cdot \dot{\mathbf{A}}_m \mathbf{d}^\circ, \quad \text{where} \quad \mathbf{d}^\circ = [\mathbf{I} - \mathbf{A}^\circ + \mathbf{Q}^\circ]^{-1} (\mathbf{p}_0 - \mathbf{q}_0^\circ). \quad (\text{SI.35})$$

All the arguments used to derive eq. (SI.35) can be used for $\partial \pi(\mathbf{0}) / \partial \delta_f$, and we find $\partial \pi(\mathbf{0}) / \partial \delta_f = \alpha \cdot \dot{\mathbf{A}}_f \mathbf{d}^\circ$. Hence,

the fixation probability to the first order in selection intensity is

$$\pi = \alpha p_{m,0} + (1 - \alpha) p_{f,0} + \delta_m \alpha \cdot \dot{\mathbf{A}}_m \mathbf{d}^\circ + \delta_f \alpha \cdot \dot{\mathbf{A}}_f \mathbf{d}^\circ + O(\delta^2). \quad (\text{SI.36})$$

The entries of \mathbf{d}° can be interpreted in terms of mean coalescence times in the resident population. To see this, we first note that if the expected initial frequency of the mutant is the same in males and females, then $p_{m,0} = p_{f,0} = p_0$, which is equivalent to assuming that mutation rate is the same in males and females. Then, if the mutant arose as a single copy, $p_0 = 1/(2N)$, where $N = N_m + N_f$, and we have $\mathbf{p}_0 - \mathbf{q}_0 = (0, 0, -1/(2N), -1/(2N), \dots, -1/(2N))^T$. In this case, element d_i° for $i \geq 3$ of \mathbf{d}° is

$$d_i^\circ = -T_{(i)}/(2N), \quad (\text{SI.37})$$

where $T_{(i)}$ is the mean coalescent time into a single individual of a set of gene lineages initially residing in state i (Lehmann and Rousset 2009, eqs. A-28 & A-29). State here refers to the configuration of the sampled gene lineages, which are given by the entries of \mathbf{p}_t , e.g., for $i = 3$, if the third entry of \mathbf{p}_t corresponds to η_t , the probability that an individual's paternal and maternal alleles are both mutant, so $d_3^\circ = -T_{(3)}/(2N)$, where $T_{(3)}$ is the expected number of generations taken for the paternal and maternal genes of an individual to coalesce.

Substituting for $\alpha = 1/2$ (for an autosomal gene) and for matrices $\dot{\mathbf{A}}_m$ and $\dot{\mathbf{A}}_f$ into eq. (SI.36), the probability of fixation of a single copy mutant ($p_{m,0} = p_{f,0} = 1/(2N)$) can be expressed as eq. (1) in the main text, where if $\mathbf{p}_t = (p_m, p_f, \eta, \kappa_m^\sigma, \kappa_c^\sigma, \kappa_f^\sigma, \kappa_m^\circ, \kappa_c^\circ, \kappa_f^\circ, \rho_m^\sigma, \rho_c^\sigma, \rho_f^\sigma, \rho_m^\circ, \rho_c^\circ, \rho_f^\circ, \dots)^T$, the sex-specific weights K_m and K_f are given by

$$\begin{aligned} K_m &= \frac{1}{4} \left(1 - \frac{1}{N_m}\right) \left[-h \left(\frac{d_4^\circ + d_7^\circ}{2} \right) - (1 - 2h) \left(\frac{d_{10}^\circ + d_{13}^\circ}{2} - d_3^\circ \right) \right] \\ K_f &= \frac{1}{4} \left(1 - \frac{1}{N_f}\right) \left[-h \left(\frac{d_6^\circ + d_9^\circ}{2} \right) - (1 - 2h) \left(\frac{d_{12}^\circ + d_{15}^\circ}{2} - d_3^\circ \right) \right], \end{aligned} \quad (\text{SI.38})$$

with d_i as the i th entry of the vector \mathbf{d}° defined in eq. (SI.35). This shows that K_m and K_f may be interpreted in terms of coalescent times for sampled genes (eq. SI.37). Alternatively, using eq. (SI.21), we see that K_m and K_f can be interpreted as the expected covariance between genotype and phenotype in males and females respectively, cumulated over the neutral segregation of the mutant

$$K_u = \frac{1}{2} \frac{1}{2N} \sum_{t=0}^{\infty} K_{u,t} = \frac{1}{4} \frac{1}{2N} \frac{1}{\delta_u} \sum_{t=0}^{\infty} \mathbb{E}^\circ [\mathbf{C}[p_{ui,t}, z_{ui}]] \quad (\text{SI.39})$$

where the sum runs from the appearance to the eventual fixation or loss of the mutant.

Probabilities of sibships of three individuals. Until now, all our results hold for any arbitrary population size, but this implies tracking many gene associations. Indeed, as eqs. (SI.22) - (SI.29) show, the iteration of eq. (SI.18) over multiple generations depends on the six probabilities of sibships over two individuals, Θ_x^σ and Θ_x° ($x \in \{m, c, f\}$), and the eight probabilities of sibships over three individuals Ξv_w^σ and Ξv_w° ($v \in \{2, 3\}$, $w \in \{m, f\}$). Therefore,

K_m and K_f (eq. SI.38) also depend on these fourteen probabilities. As we show below, we can significantly reduce the number of necessary probabilities of sibships by approximating the probabilities of sibship of three individuals Ξv_w^{σ} and Ξv_w° as functions of the probabilities of sibship of two individuals Θ_x^{σ} and Θ_x° when we only consider the first order effects of finite population size $O(1/N)$.

The probability that three randomly sampled adult males have the same father is $\Xi 3_{3m}^{\sigma} = E^{\circ}[\sum_i^{N_m} \binom{W_{mi}^m}{3} / \binom{N_m}{3}]$. In the absence of phenotypic differences, each male has the same distribution of reproductive output and $\Xi 3_{3m}^{\sigma} = 1/((N_m - 1)(N_m - 2))E^{\circ}[W_{mi}^m{}^3 - 3W_{mi}^m{}^2 + 2W_{mi}^m]$. If we assume that the distribution for W_{mi}^m is sufficiently well-behaved, and that the number of adult descendants of a male stays bounded as populations size (N) tends to infinity (or that $E^{\circ}[W_{mi}^m{}^x]$, $x \geq 0$, remains bounded as $N \rightarrow \infty$), we find that none of the terms in $\Xi 3_{3m}^{\sigma}$ are of order $1/N$ or more, i.e. $\Xi 3_{3m}^{\sigma} = 0 + O(1/N^2)$, so the probability that three randomly sampled adult males have the same father can be approximated to being zero when N is large. Similarly, we find that all probabilities of sibship three genes in the same individual are approximately zero, $\Xi 3_x^{\sigma} = \Xi 3_x^{\circ} = 0 + O(1/N^2)$ for $x \in \{3m, 3f, 2m, 2f\}$.

Rather than calculating $\Xi 2_{3m}^{\sigma}$ the probability that out of three males only two have the same father directly, it is easier to consider the probability that out of three males, none have the same father. These two probabilities are related by $1 - \Xi 3_{3m}^{\sigma} - \Xi 2_{3m}^{\sigma} = 1 - \Xi 2_{3m}^{\sigma}$ (since $\Xi 3_{3m}^{\sigma} = 0 + O(1/N^2)$). The probability that out of three males, none have the same father is given by the expected value of the ratio of the number of ways three individuals may be sampled from the male offspring of three different adult males to the number of ways of sampling three males out of the entire male population $1 - \Xi 2_{3m}^{\sigma} = [\sum_{i,j,k}^{N_m} W_{mi}^m W_{mj}^m W_{mk}^m / \binom{N_m}{3}]_{i \neq j \neq k \neq i}$, which after taking the sum and denominator outside reduces to $E^{\circ}[W_{mi}^m W_{mj}^m W_{mk}^m]_{i \neq j \neq k \neq i}$. Again by assuming that the number of adult descendants of a male stays bounded as populations size tends to infinity, using the delta method (Oehlert 1992), and observing that $E^{\circ}[W_{mi}^m] = 1$, we obtain $1 - \Xi 2_{3m}^{\sigma} = 1 + 3C^{\circ}[W_{mi}^m, W_{mj}^m]_{i \neq j} + O(1/N^2)$.

The covariance term $C^{\circ}[W_{mi}^m, W_{mj}^m]_{i \neq j}$ may be expressed in terms of Θ_m^{σ} . The probability that two males do not have the same father is, by definition, $1 - \Theta_m^{\sigma}$, but it is also given by $E^{\circ}[\sum_i \sum_{j \neq i} W_{mi}^m W_{mj}^m / \binom{N_m}{2}] = E^{\circ}[W_{mi}^m W_{mj}^m]_{i \neq j} = C^{\circ}[W_{mi}^m W_{mj}^m]_{i \neq j} + 1$, so that $C^{\circ}[W_{mi}^m, W_{mj}^m]_{i \neq j} = -\Theta_m^{\sigma}$. Hence substituting back into the probability that out of three males none have the same father, and solving for $\Xi 2_{3m}^{\sigma}$, we obtain that the probability that out of three males only two have the same father is

$$\Xi 2_{3m}^{\sigma} = 3\Theta_m^{\sigma} + O(1/N^2). \quad (\text{SI.40})$$

The remaining probabilities can be derived by using the same argument, and that $E^{\circ}[W_{mi}^f] = N_f/N_m$, producing

$$\begin{aligned} \Xi 2_{3f}^{\sigma} &= 3\Theta_f^{\sigma} + O(1/N^2) \\ \Xi 2_{2m}^{\sigma} &= \frac{2}{3N_m} + \frac{4}{3}\Theta_c^{\sigma} + \frac{1}{3}\Theta_m^{\sigma} + O(1/N^2) \\ \Xi 2_{2f}^{\sigma} &= \frac{2}{3} \left(\frac{2}{N_m} - \frac{1}{N_f} \right) + \frac{4}{3}\Theta_c^{\sigma} + \frac{1}{3}\Theta_f^{\sigma} + O(1/N^2). \end{aligned} \quad (\text{SI.41})$$

By symmetry, we find that the probabilities of sibship of three maternal genes are given to the order $O(1/N)$ by

$$\begin{aligned}\Xi_{2_{3m}}^{\circ} &= 3\Theta_m^{\circ} + O(1/N^2) \\ \Xi_{2_{3f}}^{\circ} &= 3\Theta_f^{\circ} + O(1/N^2) \\ \Xi_{2_{2m}}^{\circ} &= \frac{2}{3} \left(\frac{2}{N_f} - \frac{1}{N_m} \right) + \frac{4}{3}\Theta_c^{\circ} + \frac{1}{3}\Theta_m^{\circ} + O(1/N^2) \\ \Xi_{2_{2f}}^{\circ} &= \frac{2}{3N_f} + \frac{4}{3}\Theta_c^{\circ} + \frac{1}{3}\Theta_f^{\circ} + O(1/N^2).\end{aligned}\tag{SI.42}$$

So assuming the population is large, the iteration of eq. (SI.18) over many generations depends only on the six probabilities of sibships over two individuals, Θ_x° and Θ_x° ($x \in \{m, c, f\}$).

Solving for K_m and K_f in terms of the probabilities of sibships of two individuals. Having expressed the eight probabilities of sibships of three individuals in terms of the probabilities of sibships of two individuals Θ_v^u , the matrix \mathbf{A}° now only depends on these latter six probabilities of sibships, and therefore, so do K_m and K_f (eq. SI.38). Despite this simplification, solving explicitly for K_m and K_f still requires inverting a 23×23 matrix, $(\mathbf{I} - \mathbf{A}^{\circ} + \mathbf{Q}^{\circ})^{-1}$, which is computationally expensive and unlikely to yield results easy to interpret. Numerical results for K_m and K_f with arbitrary dominance are shown in fig. 4.D of the main text. However, if $h = 1/2$, only the first nine entries of \mathbf{p}_t are required to generate the expected frequency change over many generations, and hence the probability of fixation. Thus, \mathbf{A}° reduces to a 9×9 matrix. In this case, $(\mathbf{I} - \mathbf{A}^{\circ} + \mathbf{Q}^{\circ})^{-1}$ can be inverted analytically, and using (SI.38) with $h = 1/2$, K_m and K_f are as eq. (A.2) in the main text.

Probabilities of sibship of two individuals. The probability of fixation of a mutant depends on the probabilities of sibship of two individuals in the resident population. Here, the probabilities of sibship are expressed in terms of the first (μ 's) and second (ν and ρ) moments of the distribution of offspring produced by a resident male and a resident female to give table 1 of the main text.

The probability that two randomly sampled adult males have the same father, Θ_m° , is given by the expected value of the ratio of the number of ways two individuals may be sampled from the number of adult males produced by each male, to the number of ways of sampling two males out of the entire male population, i.e., $\Theta_m^{\circ} = E^{\circ}[\sum_{i=1}^{N_m} \binom{W_{mi}^m}{2} / \binom{N_m}{2}]$, where W_{mi}^m is the random variable for the number of male breeders produced by male i . In the absence of phenotypic differences in the population, each male has the same distribution for their reproductive output, so the sum may be taken out in Θ_m° , and the subscript i now denotes a randomly sampled male: $1/(N_m - 1) [V^{\circ}[W_{mi}^m] + E^{\circ}[W_{mi}^m](E^{\circ}[W_{mi}^m] - 1)]$. The expected number of male adults produced by a male in the absence of phenotypic differences, $E^{\circ}[W_{mi}^m] = 1$, so the probability that two randomly sampled adult males have the same father reduces to $\Theta_m^{\circ} = V^{\circ}[W_{mi}^m]/(N_m - 1)$. Conditioning on the number of male juveniles produced in the population, and using the law of total variance, this gives

$$\Theta_m^{\circ} = \frac{1}{N_m - 1} \left(N_m^2 V^{\circ} \left[\frac{J_{mi}^m}{J_m} \right] + E^{\circ} [V^{\circ} [W_{mi}^m | J_{mi}^m, J_m]] \right).\tag{SI.43}$$

The second variance term in eq. (SI.43) depends on how culling or regulation is assumed to take place, which is

assumed here to occur by sampling juveniles without replacement. In this case, W_{mi}^m follows a hypergeometric distribution with N_m draws and parameters given by the realization of J_m^m , with initial probability of success J_{mi}^m/J_m and a total population size of J_m . Then, $E^\circ[V^\circ[W_{mi}^m|J_{mi}^m, J_m]] = E^\circ[N_m J_{mi}^m (J_m - J_{mi}^m)(J_m - N_m)/(J_m^2(J_m - 1))]$. Both variance terms in eq. (SI.43) are approximated omitting terms of order $1/N^2$ using the delta method. With assumption eq. (A.1) in the main text, the second variance term can be approximated as

$$\frac{1}{N_m - 1} E^\circ \left[\frac{N_m J_{mi}^m (J_m - J_{mi}^m)(J_m - N_m)}{J_m^2 (J_m - 1)} \right] \approx \frac{E^\circ[J_{mi}^m]}{E^\circ[J_m]} = \frac{\mu_{mi}^m}{\mu_T^m} = \frac{1}{N_m}. \quad (\text{SI.44})$$

Then, using the delta method with the variance operator, the first variance term in eq. (SI.43) is

$$\frac{N_m^2}{N_m - 1} V^\circ \left[\frac{J_{mi}^m}{J_m} \right] = N_m \frac{V^\circ[J_{mi}^m]}{E^\circ[J_m]^2} + O(1/N^2) = N_m \frac{\nu_{mi}^m}{\mu_T^{m2}} + O(1/N^2). \quad (\text{SI.45})$$

Finally, substituting eqs. (SI.44)(SI.45) into eq. (SI.43) gives Θ_m^{σ} in table 1 of the main text. Using the same argument, we find a similar form for the probabilities that two females have the father Θ_f^{σ} , that two males have the same mother Θ_m° and that two females have the same mother Θ_f° (see table 1 in the main text).

The probability that a male and a female have the same father Θ_c^{σ} is given by $E^\circ[\sum_{i=1}^{N_m} W_{mi}^m W_{mi}^f / (N_m N_f)]$, where W_{mi}^f is the random variable for the number of female breeders produced by male i . By conditioning on the juvenile production of every individual and using the assumption that male and female offspring are culled independently, we have $\Theta_c^{\sigma} = N_m E^\circ[J_{mi}^m J_{mi}^f / (J_m J_f)]$. The delta method is used to approximate the latter. Then, expanding about the means of J_{mi}^m, J_{mi}^f, J_m and J_f and using condition eq. (A.1) in the main text, we have

$$\Theta_c^{\sigma} = \frac{1}{N_m} + N_m \frac{C[J_{mi}^m, J_{mi}^f]}{E[J_m]E[J_f]} = \frac{1}{N_m} \left(1 + \frac{\rho_{mi}^{m,f}}{\mu_{mi}^m \mu_{mi}^f} \right), \quad (\text{SI.46})$$

where $\rho_{mi}^{m,f} = C[J_{mi}^m, J_{mi}^f]$ is the covariance between the number of male and offspring juveniles fathered by a male. Using a similar argument, the probability that a male and a female have the same mother is found as in table 1 of the main text.

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