March 17, 1942

Dear Mather,

I wonder if you would care to look through for me the enclosed note on Sturtevant's sex ratio factor. I may easily have forgotten some of the relevant facts, as it is written wholly from memory.

Probably also you can suggest better ~~numbers~~ numerical values than I have used for the ratios k and p.

I suppose no one has made mating tests which would either indicate or exclude such a preference as I am inclined to infer.

Yours sincerely,

March
1942

The sex-ratio factor [redacted] situated in the X-chromosome. It is said to be without effect on the appearance or fertility of females, but to alter the sex[redacted]o of sperm from ~~approximately~~ 1 X : 1 Y to 1 X : k Y

Equilibrium in the frequency of the sex-ratio factor thus requires that males affected by it shall have fewer offspring than other males in the ratio $(1+k):2$

If an X carrying the mutant is represented by X', there are five distinct genotypes

Females	Males
XX	XY
XX'	
X'X'	X'Y

These will, however, contribute unequally to future generations. If the relative frequencies of the two types of male are as $q:p$, it is easy to see that those of the three types of female are as $q^2:2pq:p^2$.

Now, let the contributions to future generations of the three types of female and of the two types of male be as $u : v : w : x : y$. Then, equating the contribution of each genotype to that of its progeny, it follows that, if c is some undetermined constant,

$$\begin{aligned} cu &= qu + pv + qx + pkx \\ 2\,cv &= q(u+v) + p(v+w) + (q+pk)(x+y) \\ cw &= qv + pw + (q+pk)y \end{aligned}$$

Obviously, then

$$2v = u + w.$$

Next, considering the output of the whole population, we may multiply the equations by q^2, pq and p^2 and add, finding

$$c(q^2u + 2\,pqv + p^2w) = q^2u + 2\,pqv + p^2w + (q + pk)(qx + py)$$

or $$(c-1)(qu + pw) = (q + pk)(qx+py)$$

Moreover, for the population as a whole the total value of the males must be equal to that of the females, so that

$$qu + pw = (q + pk)(qx + py)$$

or, $$c = 2.$$

Hence, subtracting the third equation from the first

$$2(u - w) = u - v + (q + pk)(x - y)$$

or $$\frac{u - w}{q + pk} = \frac{x - y}{1\tfrac{1}{2}}$$

Similarly, considering the progeny of the two types of males, we may write

$$c'x = qu + pv + qx + py$$

$$c'y = qv + pw + k(qu + py)$$

Multiplying by q and p and adding, these give

$$c'(qx + py) = qu + pw + (q + pk)(qx + py)$$

whence

$$c' = 2(q + pk),$$

and from the difference between the equations

$$2(q + pk)(x - y) = \tfrac{1}{2}(u - w) + (1 - k)(qx + py)$$

or $$2\tfrac{1}{2}(u - w) = (1 - k)(qx + py)$$

In all, it now appears that

$$\frac{u - w}{q + pk} = \frac{x - y}{1\tfrac{1}{2}} = \frac{1 - k}{2\tfrac{1}{2}(q+pk)}(qx + py) = \frac{1 - k}{2\tfrac{1}{2}(q+pk)^2}(qu + pw)$$

from which all the ratios may be obtained, i.e.

$$\frac{x}{3q+2(q+pk)} = \frac{y}{3k+2(q+pk)} = \frac{u}{(q+pk)\{2+3(q+pk)\}} = \frac{w}{\quad}$$

$$\frac{v}{(q+pk)\{1+k+3(q+pk)\}} = \frac{w}{(q+pk)\{2k+3(q+pk)\}}$$

The numbers of the five genotypes in equilibrium in the population are

Females		Males	
Genotype	frequency	Genotype	frequency
XX	Nq^2	XY	$Nq(q+pk)$
XX'	$2Npq$		
X'X'	Np^2	X'Y	$Np(q+pk)$
Total	N		$N(q+pk)$

Corresponding with these, we may set out the contributions of these genotypes to a remote future generation

Genotype	Total value	Genotype	Total value
XX	$q^2\{2+3(q+pk)\}$	XY	$q\{3+2(q+pk)\}$
XX'	$2pq\{1+k+3(q+pk)\}$		
X'X'	$p^2\{2k+3(q+pk)\}$	X'Y	$p\{3k+2(q+pk)\}$
	$5(q+pk)$		$5(q+pk)$

Although the sexes are produced in ~~equal~~ unequal numbers, their contributions to future ancestry are necessarily equal.

The possibility of sexual selection requires a knowledge of the value of the progeny to be expected from each possible type of mating. Taking $2(1+k)$ offspring from each mating, these are

Female parent	Male parent XY	Male parent X'Y
XX	$(1+k)\{3+4(q+pk)+3(q+pk)^2\}$	$6k+2(1+3k)(q+pk)+6(q+pk)^2$
X'X'	$(1+k)\{3k+(3+k)(q+pk)+3(q+pk)^2\}$	$6k^2+8k(q+pk)+6(q+pk)^2$
Average	$2(1+k)(q+pk)\{3+2(q+pk)\}$	$4(q+pk)\{3k+2(q+pk)\}$

The progeny of an XX' ♀ being in each case half the sum of the progenies of XX and X'X' females.

For each type of female the contribution of her brood to future generations will be larger if she is fertilised by a ~~mxk~~ non-mutant than by a mutant male. On the average the advantage is in the ratio

$$\frac{(1+k)\{3+2(q+pk)\}}{2\{3k+2(q+pk)\}}$$

If k is 0.05, the ratio rises from 1.2204 when p = 0, to 6.51 when p = 1. If, for example, ~~Thus if k = 0.1, and p = 12%, the ratio would be~~ *p is 12%, the ratio is 1.3078. Thus the contribution of females of this to future generations would be 30.78% greater if they are fertilised by normal, than they if they were fertilised by mutant males*

$$\cancel{\frac{(1.1)(4.784)}{2(2.084)} = 1.2626}$$

~~The contribution to future generations of females which are fertilised by non-mutant males is thus 26.26% greater than that of the same females if fertilised by mutant males.~~ If, therefore, ~~the~~ the female possesses any power of discrimination, by which the two types of male may be distinguished, they will be strongly selected so as to prolong the progress of courtship by mutant males, and so to ~~ensure~~ increase the probability of fertilisation by ~~more~~ non mutants. Equilibrium will be established when the chances of mating of a mutant male are less than those for a non mutant in the ratio(1+k):2.

How powerful a differential reaction on the part of the females could bring this about must depend greatly on the population density. It may be inferred that the mutant gene is chiefly maintained in sparse populations, so far as these are self supporting, and is normally being eliminated among the denser populations.