25 October 1932.

Professor C.G. Darwin, F.R.S.,
14 Heriot Row,
EDINBURGH.

Dear C.G.:

I believe I never persuaded you entirely that my runaway process in sexual selection would work. I have been re-reading your notes on the point in the copy of my book you were good enough to send me and I think I may be able to get over your difficulty. I will take your note as my text:-

"There are always females who don't care and take ugly cocks, and these should breed just as well. By hypothesis there are too few hens to go round, so all get cocks";

and again:-

"As I understand the argument, the two agencies are cock beauty and hen taste, and each reinforces the other. But if there are fewer hens I don't see how hen taste gets reinforced".

I believe I missed getting my point taken by you by thinking in terms of two generations whereas you wanted to see how it worked in each single generation, and of course one must be able to do that, Take x for cock beauty, and y for hen taste.

during perturbation of a "steady state".

These will vary about some means $\bar{x}$ and $\bar{y}$; of which $\bar{x}$ will not matter, for there is no natural zero for this measurement, but $\bar{y}$ will, for $y = 0$ would represent indifference, and $\bar{y}$ the average intensity of preference. We may suppose for convenience that x and y are genetic values so that their averages in the offspring are the averages for the two parents, and that for each the scale of measurement is so chosen that the mean values of $(x - \bar{x})^2$ and $(y - \bar{y})^2$ are both unity. They may be correlated to a degree which must be determined from the problem so we may put r for the average value of $(x - \bar{x})(y - \bar{y})$

We might suppose beauty to be measured objectively e.g. by the length of feathers in a ruff, but taste will have to be measured by actual performance. A hen with no taste would mate at random, i.e., on the average of a number of trials, the average x of the cock she mates with is $\bar{x}$. A selective hen will lose some opportunities of mating with ugly cocks and will score a higher average. On our scale of measurement I will say that her value is y if the average beauty of the cock she chooses is $\bar{x} + ky$. k is a datum depending on powers of discrimination, opportunities for choice, etc.

If a cock with specification x_1, y_1 mates with a hen specified by x_2, y_2 the offspring vary about the average

$$\frac{x_1 + x_2}{2}, \qquad \frac{y_1 + y_2}{2}$$

The only hypothesis about heredity we need is that within this progeny x and y are uncorrelated; if this is true, then ~~so that~~ the mean product r in the progeny generation will be merely

$$\frac{1}{4}(x_1 - \bar{x} + x_2 - \bar{x})(y_1 - \bar{y} + y_2 - \bar{y})$$

averaged over all matings. If this is the same as in the previous generation we can find r, for the average value ~~ø~~ of

$$(x_1 - \bar{x})(y_1 - \bar{y}) = r \quad \text{and} \quad (x_2 - \bar{x})(y_2 - \bar{y}) = r$$

while for the rest

$$(x_1 - \bar{x})(y_2 - \bar{y}) = k y_2 (y_2 - \bar{y}) = k \quad \text{and} \quad (x_2 - \bar{x})(y_1 - \bar{y}) = \cancel{r}\, r^2 k$$

as appears from averaging the kinds of cock which any particular hen x_2, y_2 will mate with.

It appears then that

$$2r = k(1 + r^2) \quad \text{or} \quad r = \frac{1 - \sqrt{1 - k^2}}{k},$$

and a selection which raises the average of x by $\frac{1}{2} k \bar{y}$ in each generation must raise the average of y by $\frac{1}{2} k r \bar{y}$ i.e. $\bar{y}$ increases in geometrical progression, supposing k, and therefore r, to be constant. Of course in this I have ignored all checks, some of which may work slightly from the start, while others will certainly come in powerfully later.

Let me know if I have made any headway, as I found myself entirely dissatisfied with my inability to get the argument across, and I hope the point that x and y must be correlated may remove the difficulty you feel.

Yours sincerely,