7   June 1930.

Major Leonard Darwin, Sc.D.,
    Cripps's Corner;
        Forest Row,
            Sussex.

Dear Major Darwin,

I must write more clearly about the non-genetic early nesting theory, especially as I am sure I got it from you.

Supposing the date at which breeding phenomena are initiated, e.g. by migration etc., to depend on the female only, there must be an optimum date, appropriate to the average bird, for these phenomena to start.   The date of starting is partly determined by a heritable variate x, partly by other circumstances.   We must suppose x to vary among different females and, to make it more concrete we might imagine it to be determined experimentally by giving a number of young females exactly the same nutritional and climatic experience and note the date at which they show the first sign of the reproductive sequence.

Now my first point is that the average value of x must be the same generation after generation, so that the average number of offspring left by females with a high x, and therefore congenitally prone to start breeding early, must be the same as that of females with low x, congenitally prone to start breeding late.   Of course I don't doubt that the medium values are favoured over the extremes, but the net effect of selection on the mean value of x must be zero if the distinction between a winter feeding period and a spring breeding period is maintained at all.   How then can it be that the males who breed early gain an advantage? Partly because more of them breed, (this is my suggestion in respect of death-rates), and partly, and this I think was your father's theory, because those that do actually breed early (as contrasted with those who are only congenitally prone so to breed) really do leave more offspring than those breeding later.   This is possible if we imagine the actual breeding date to be modified by environmental factors which are also influential in favouring reproduction so that a group of females having identically the same values of x,

might start migrating at dates from 15th. to 30th. March, those moving earliest being destined on the average, by reason of their better nutritional condition, to rear the largest families; but no larger perhaps than are reared by birds with a lower value of x who start on March 30th.

Here is a chart, 6^4 means 4 pairs of birds worth rearing 6 young. If on consideration you think this is a fair representation of your father's theory, I should like to put it in any further editions so as to make it explicit.

You will see that the selection for increasing x due to the larger families of those mated early is exactly counterbalanced by the selection for small x among those breeding at a given date.

The enclosed letter might amuse you, it shows well what a blind spot I am up against.

Yours sincerely,

Enclosures:
1 letter
1 copy of reply (RAF).

	ACTUAL STARTING DATE.									Average
					7^1	6^4	5^6	4^4	3^1	5
				7^4	6^{16}	5^{24}	4^{16}	3^4		5
x			7^6	6^{24}	5^{36}	4^{24}	3^6			5
		7^4	6^{16}	5^{24}	4^{16}	3^4				5
	7^1	6^4	5^6	4^4	3^1					5
	7	$6\frac{1}{2}$	6	$5\frac{1}{2}$	5	$4\frac{1}{3}$	4	3_ε	3	Average

ROTHAMSTED EXPERIMENTAL STATION,

HARPENDEN, HERTS.

Director:
SIR JOHN RUSSELL, D.Sc., F.R.S.

STATISTICAL DEPT.
R. A. FISHER, Sc.D., F.R.S.
J. WISHART, D.Sc.
J. O. IRWIN, M.A., M.Sc.

27 June 1930.

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      Forest Row,
         Sussex.

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Now my first point is that the average value of x must be the same generation after generation, so that the average number of offspring left by females with a high x, and therefore congenitally prone to start breeding early, must be the same as that of females with low x, congenitally prone to start breeding late. Of course I don't doubt that the medium values are favoured over the extremes, but the net effect of selection on the mean value of x must be zero, if the distinction between a winter feeding period and a spring breeding period is maintained at all. How then can it be that the males who breed ~~early~~ gain an advantage? Partly because more of them breed, (this is my suggestion in respect of death-rates), and partly, and this I think was your father's theory, because those that do actually breed ~~early~~ (as contrasted with those who are only congenitally prone so to breed) really do leave more offspring than those breeding later. This is possible if we imagine the actual breeding date to be modified by environmental factors which are also influential in favouring reproduction so that a group of females having identically the same values of x,

[handwritten margin note:] No, I really necessarily, before the optimum date × for the average bird as soon as possible after the optimum date (then)

might start migrating at dates from 15th. to 30th. March,
those moving earliest being destined on the average, by
reason of their better nutritional condition, to rear the
largest families; but no larger perhaps than are reared
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Yours sincerely,

R. A. Fisher

Enclosures:
    1 letter
    1 copy of reply (RAF).
    1 Chart.

ACTUAL STARTING DATE. →

	7	6½	6	5½	5	4½	4	3½	3	Average *effort*
					7^1	6^4	5^6	4^4	3^1	5
				7^4	6^{16}	5^{24}	4^{16}	3^4		5 − ?10
				14	12	10	8	6		
x ↓			7^6	6^{24}	5^{36}	4^{24}	3^6			5 − ?15
			21	18	15	12	9			
		7^4	6^{16}	5^{24}	4^{16}	3^4				5 − 10
		14	12	10	8	6				
	7^1	6^4	5^6	4^4	3^1					5

Average *effort*	7	6½	6	5½	5	4½	4	3½	3	Average
			10	$12\frac{12}{13}$	$13\frac{3}{7}$					

horizontal
differences in *these* rows are due
to Environment.

quite right, I think. LD.