DIALLEL CROSSINGS WITH THE DOMESTIC FOWL.

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IN three previous papers (1919, 1; 1919, 2; 1921) I have described the results of diallel crossings with the common trout (*Salmo trutta* L.)[1]. The task being to classify or to value a certain number of individuals in regard to some *quantitative* character, i.e. a character which may be analysed by counting, measuring or weighing—the manner of proceeding in diallel crossing is as follows. Each female is paired with each male, care being taken that the offspring is raised under external conditions as uniform as possible. If there are a females and b males $a \times b$ different combinations will occur among the offspring of the diallel crossings. Within each offspring-combination the character in question is analysed —by counting, measuring, or weighing each individual—and then the average value of all individuals is determined. *It is with such average values*—determined by analysing a number of individuals, as great as possible; and developed under external conditions as uniform as possible —*that the method of diallel crossings operates.*

Already the first experiments showed the necessity of distinguishing clearly between the purely *personal* value of an individual—in the case under consideration the number of vertebrae that may be counted in the individual at hand—and the *generative* value, i.e. the value it imparts to its offspring. The generative value of an individual may differ widely from its personal value, so that from the latter few or no conclusions can be drawn with regard to the former. This particular fact is largely responsible for the difficulties which the work with quantitative characters entails, not only upon the student of genetics, but also upon the practical breeder. It is the generative value which both of them need to know, the geneticist when he has to classify the offspring-individuals from a crossing experiment, and the breeder when he has to select—

[1] "La valeur de l'individu à titre de générateur, appréciée suivant la méthode du Croisément diallèle" (*C.R. Laboratoire Carlsberg*, Copenhagen, 1919); "Diallel crossings with trout (*Salmo trutta* L.) (*Journal of Genetics*, IX. 1919); "The numerical significance of fused vertebrae" (*C.R. Laboratoire Carlsberg*, Copenhagen, 1921).

perhaps among a number of individuals personally very similar—those best fit to breed from.

A frequently occurring special case of diallel crossings is when $b=1$, i.e. when a single male—let us call it x—is paired with a females. $1 \times a = a$ different offspring-combinations will then arise. Each of these will, provided a sufficiently large number of individuals be present, exhibit a full representation of all the different gametes possessed by the father x, which is common to all of them. The a offspring-combinations, therefore, differ only in those gametes coming from each of the a mothers. From this it follows that we are able to compare directly the average values of the a offspring-combinations, and to get thereby an expression of the differences between the generative values of the females, the common male x cancelling, so to speak, in such a comparison. These differences are thus independent of the father common to all offspring-combinations. After pairing a number of females with the same male we can therefore determine the differences between their generative values irrespective of the male, and similarly, we may, of course, determine the differences between a number of males, after having paired them with the same female. *This is the leading principle in the method of diallel crossings.*

When this method was described, in 1919, we did not know the way in which such quantitative characters are inherited, and the manner of proceeding had therefore necessarily to be entirely empirical[1]. In consequence of its principle the method, however, is *self-checking*. When pairing the same a females, which were paired with x, with other males (y, z, v), and calculating the differences between the values of the females in the same way as after the first pairing with male x, *the same differences were found in all cases.* In this way the *automatic checking of the method yielded experimental evidence of the rightness of the principle of diallel crossings.*

In our trout experiments we were dealing with heterozygous individuals the genetic structure of which was entirely unknown. Nevertheless it proved possible to determine the differences between the various individuals—in other words to classify them—with no less certainty than when classifying a number of Pure Lines. On that subject I refer to my previous papers (1919, 1 and 1919, 2).

With a character like "number of vertebrae" we have to do with so-called *integrated variates,* which are generally realised only as integral

[1] Since then I have been able to clear up the genetic behaviour of the number of vertebrae. A detailed report is expected to appear shortly.

numbers. The diallel crossings showed that not only the generative values, or the differences between them, may be any fraction, but further, that the *personal values may be fractions*. Certain "fusions" of two vertebrae in the trout thus had to be interpreted as "attempts" at realising fractional parts of a vertebra (1921). This would seem to mean that no fundamental difference exists between "integrated variates" and "class-variates."

When it was established that the method of diallel crossings could be applied to characters as different as the number of vertebrae in fishes and the length of petals in a species of *Nicotiana* (1919, 1) there was reason to believe that the method might be generally employed in the study of quantitative characters. It appeared to me, however, of importance to have the method tested for as many species as possible. After having tried various vertebrates I selected the domestic fowl which proved to be a useful subject. The experiments were made in 1919 and 1920 in the Carlsberg Laboratory, Copenhagen, and the character examined was again the number of vertebrae. This number proved to vary more than was expected. As a matter of fact, in our small stock we found a range of 6, the number of vertebrae varying from 39 to 44.

The countings were made by Mr Vilh. Ege, M.Sc., who has worked out a very reliable technique.

Two cocks (x and y) and five hens (a, b, d, e, f) were used in the experiment. Most of them were mongrels; y was a Faverolles cock and e a Plymouth Rock hen.

Table I shows the result of the diallel crossings. For each of the ten (2×5) offspring-samples the number of vertebrae in each individual chicken is shown graphically. The average numbers of vertebrae of the various offspring-combinations are given in Table II, the figures in each case being denoted by the symbols of the parents, thus:

$$\frac{x+a}{2} = 40{\cdot}53 \text{ etc.}$$

By means of the ten equations

$$\left(\frac{x+a}{2} = 40{\cdot}53, \ \frac{y+a}{2} = 41{\cdot}21 \text{ etc.}\right)$$

we are, in the manner described in my previous papers, able to calculate the generative values of the 7 parents and to compare them with their personal values. Several of the animals being, however, still alive, we do not know all the personal values as yet and we may therefore better postpone such a comparison until all the figures in question are available (for the hens e and f the personal values are given in the foot-note on page 245).

TABLE I.

Diallel crossings of two cocks (x and y) with five hens (a, b, d, e, f). The graphs show the number of vertebrae in each individual of the offspring.

Females		Male x		Male y
a	43		43	
	42	0	42	00000000
	41	00000000000000000000	41	0000000000000
	40	000000000000000000	40	000
	39	0	39	
b	43		43	0
	42		42	00000000000
	41	00000000000000000000000000000	41	00000000000
	40	0000	40	
	39		39	
d	43		43	0
	42	00000	42	00000000000
	41	000000000000000000000000000000000000	41	0000000000
	40	0000000	40	
	39		39	
e	43		43	
	42		42	000
	41	00000000000000000000000000	41	000000000000
	40	00000000000000000000000	40	
	39		39	
f	43		43	000
	42	000000	42	000000000000000000000000
	41	000000000000000000000000000	41	000000000
	40	00	40	0
	39		39	

TABLE II.

Average numbers of vertebrae in the ten offspring-combinations (first and second columns) and difference between the generative values of cocks y and x (third column).

		$\frac{y-x}{2}$
$\frac{x+a}{2}=40{\cdot}53$	$\frac{y+a}{2}=41{\cdot}21$	0·68
$\frac{x+b}{2}=40{\cdot}88$	$\frac{y+b}{2}=41{\cdot}57$	0·69
$\frac{x+d}{2}=40{\cdot}96$	$\frac{y+d}{2}=41{\cdot}59$	0·63
$\frac{x+e}{2}=40{\cdot}53$	$\frac{y+e}{2}=41{\cdot}20$	0·67
$\frac{x+f}{2}=41{\cdot}11$	$\frac{y+f}{2}=41{\cdot}78$	0·67

For the time being we shall therefore content ourselves with an examination of the applicability of the method to the present subject—number of vertebrae in the domestic fowl—in other words to examine whether the method already tested for other species also holds good in the present case.

As the two cocks x and y both enter into all 5 crossings, the differences between their generative values have been determined 5 times, each determination being made independently of the other.

In Table I the offspring-combinations of a vertical row have the same father (x and y) and those of a horizontal row have the same mother (a, b, d, e, f). Already an inspection of the graphs shows that cock y must have a greater generative value than cock x. Suppose the property of imparting a great number of vertebrae to its offspring is a valuable character, we are enabled by our experiment to classify cock y as being superior to cock x.

In Table II we find numerical expressions for the five determinations of $\frac{y-x}{2}$, that is to say of the differences between the generative values of y and x. It must be remembered that the determinations were made independently of each other, by means of five different hens.

We see that the five values for $\frac{y-x}{2}$ *vary between* 0·63 *and* 0·69. In spite of the number of offspring-individuals in some cases being but small, *these values agree so well that no reasonable doubt can exist that the principle of diallel crossings holds good here as in the previously examined cases.*

Provided that the character in question had been of practical importance itself, or if another character of practical importance, e.g. a great egg-laying capacity were associated with a high number of vertebrae, our valuation of the two cocks would have been of practical importance. Through a direct examination of the personal values of the two animals little or nothing could have been concluded in regard to their generative values[1].

Note added during printing. Cock y died on 14/3/1922, and on examination proved to possess 42 vertebrae, i.e. the same number as cock x which died in 1920. This yields a fresh instance of the fact that two personally identical individuals may differ widely in regard to the generative values. The difference between the generative values of cocks y and x, or rather, the half difference $\left(\frac{y-x}{2}\right)$, appears from Table II.

[1] I may mention here that hens e and f both proved to possess 40 vertebrae (personal values). From Table II it appears that they are far from being identical in regard to generative values. The difference between the latter amounts to no less than

$$1{\cdot}16\left(\frac{f-e}{2}=0{\cdot}58\right).$$