A MANUAL

OF

MENDELISM

by

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TO

THE LATE JAMES BRODIE, M.A.,

MATHEMATICAL MASTER IN FORFAR ACADEMY

"Aye be true to the line."

PREFACE

THE first edition of this volume was criticised for three or four things: it was called a Manual; it was dedicated to a teacher of mathematics; it said nothing about chromosomes and nothing about the "presence and absence" theory. These defects, if defects they be, are all repeated in this edition. And these are the reasons:

When first I heard that Mendelism was upsetting some of our old theories in stock-breeding, I had to try to understand it and expound it to students, most of whom, for the rest of their lives, would have to do with stock-breeding or plant-breeding, or with both. Few of these students would have to become specialists in Mendelism; they would have other work to do. So, what they wanted was a good "grounding" in "the principles." Any who had to specialise, having been shown the way up the main stem, could afterwards find their way to the "higher" branches for themselves. These students were unusually capable young fellows with two years' good training in physics and chemistry and the natural sciences behind them, and, so, were worthy of being asked to give, and capable of giving, useful criticism of what was put before them. Thus, we studied Mendelism together.

One of our first troubles, for few of us knew Greek, was the Greek-derived words which, by this time, had become attached to the subject. For these we substituted, where we could, others which were just as accurate and could be understood and used by ourselves and others with less difficulty. If any of us, later on, were to have to teach the subject or discuss it with crop-growers and stock-breeders, as most of us would, these lang-nebbit words would at once hinder both the giving and the receiving of knowledge.

Another trouble was the "presence and absence" theory. It led us into more than one fog. Once we found two absences claiming possession of the same place at the same time. Someone asked "What is an absence?" The question was not easily answered, and, when we thought it out, we concluded that there was no answer. A body—and a factor, though small, is a body—cannot move from one place to another and leave its absence in the place it left. When we say that, at a certain place at a certain time, somebody was "conspicuous by his absence," we use a figure of speech and say somebody was somewhere else; but, if we mean that the same somebody's absence was at that certain place at that certain time, we mean nonsense. What, then, were we to do? The absences we were discussing were the recessives of two dominant characters which were clearly enough defined. The nature of the absences could neither be defined nor even imagined. "Do as the professor of mathematics would do," said someone, "and call them x and y." So we gave them "unknown" symbols, and solved that and other problems.

We never troubled about the chromosomes. We never needed. It was not till we had been given a reprint of Mendel's original paper that we knew that Mendel had established a law. Not a few Mendelians do not yet know that Mendel did this, while others, who are aware there is a law, do not know what it is. With this law and a few simple corollaries we managed to solve the problems which came before us, even problems in sex- and non-sex linking. It might have been interesting to have traced the factors back to their own chromosomes and to have found that some, when they happen to foregather on the same chromosome, are unwilling to part company again; but would this have made the problems more easily solved? Would it not have added to their complications?

This volume, which is the outcome of our studies, was written for others who, like ourselves, might some day need or wish to have a working knowledge of Mendelism. It is not called a primer: it is too big for that; it is not called a compendium or a thesaurus: it is too small for that; but just a manual: a thing to be stuffed in the pocket or held lightly in the hand. It is dedicated to a teacher of mathematics for two reasons: one to say how thankful his old boys are to James Brodie, the other to indicate that he who wishes to understand and use Mendelism will not get very far without arithmetic.

HARPENDEN,
February, 1929.

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A MANUAL OF MENDELISM

I

MENDEL'S EXPERIMENTS

Gregor Mendel, who was born in 1822, sought and obtained admission, when he left school, to the King's Cloister at Brünn, to be trained as a teacher. He was ordained a priest in 1847, went to Vienna, from 1851 to 1853, to study mathematics, physics, and the natural sciences; and returned to the King's Cloister, of which, in 1868, he became prelate.

In the Cloister garden at Brünn, Mendel became an experimental plant-grower, obviously with the intention of discovering whether plants could be modified by cultivation. He found they could not; for he remarked one day to Dr. von Niessl, to whom he had shown some which had been cultivated for some years: "This much I *do* see, that nature cannot get on further with species-making in *this* way. There must be something more behind."

Mendel then turned to hybrids and hybridisation. In this subject botanists had already been at work, but their work had not been carried far enough. Hybrids had been bred and observed, some had been bred from for several generations, and it had been found, for example, that, among their descendants, the hybrid kinds decreased, while the pure kinds increased. But, so far, nobody had made a systematic classification and count of the whole of any hybrid's descendants through several generations; and, arguing that, till this were done, the law governing the reproductive behaviour of hybrids was not likely to be discovered, Mendel decided to do what other investigators had either neglected or overlooked. He decided to grow and breed from a number of hybrids through as many generations as might be necessary, and, that his work should have a reasonable chance of success, decided also that:

1. The experimental parent plants should possess constant (*i.e.*, non-varying) differentiating characteristics.

2. The hybrids should be protected or readily protectable from strange pollen during the flowering period; and that

3. The hybrids and their descendants in the next generations should suffer no serious loss in fertility.

In Mendel's opinion, the plant which fulfilled these conditions best and was, at the same time, easily cultivated was the ordinary edible pea. So the seeds of 34 different varieties were bought from seedsmen and, to make sure that they bred true, grown separately for two years before any experiments were begun. Out of these 34 varieties, 22 were retained and stocks grown on so long as the experiments lasted. All continued to breed true.

For the first series of experiments, 14 of the 22 varieties were chosen which could be arranged in pairs, in each of which one member differed from its fellow in one well-defined pair of characters. The following table shows the characters in which the members of the seven pairs differed:

In One Member.	*In the Other.*
1. The seed-coat was round and smooth.	The seed-coat was wrinkled.
2. The seed had yellow "albumen."	The seed had green "albumen."
3. The seed-coat was coloured.[1]	The seed-coat was white.
4. The pods were plain.	The pods were constricted.
5. The unripe pods were green.	The unripe pods were yellow.
6. The flowers were axial.	The flowers were terminal.
7. The stems were 6 to 7 feet long.	The stems were ¾ to 1½ feet long.

The two members of each of these seven pairs were crossed with each other: reciprocal crosses being made in all cases. For example, plants having round seeds were crossed with plants having wrinkled seeds, sometimes the one kind being the male parent, sometimes the other.

When grown, the hybrids were found all to be like one or other of their parents, not like both. Those between parents having round seeds and parents having wrinkled seeds had all round seeds; those between parents having long stems and parents having short stems had all long stems; and so on. The well-defined differentiating character borne by one of the parents had, in every case, disappeared.

By way of designation, Mendel called the character carried by the hybrid the *dominant* character, that which had disappeared the *recessive*. The following table, in which the characters found to be dominant are indicated by capital letters, those found to be recessive by small, gives the number of plants crossed and the number of successful fertilisations in each of the seven pairs:

[1] Grey, grey-brown, or leather-brown.

		Plants Crossed.	Successful Fertilisations.
1. ROUND seeds	x wrinkled	15	60
2. YELLOW albumen	x green	10	58
3. COLOURED seed-coat	x white	10	35
4. PLAIN pods	x constricted	10	40
5. GREEN unripe pods	x yellow	5	23
6. AXIAL flowers	x terminal	10	34
7. LONG stems	x short	10	37

The next part of Mendel's work was that overlooked by earlier investigators, namely, to carry on for one or more generations, observe and count the hybrids' progeny and, if need be, their progeny's progeny. Accordingly, seeds of all the seven kinds of hybrids were sown and the plants grown from them, self-fertilised. When arranged and counted, their progeny were found to consist, in every case, of both the original parent kinds again, but in the proportion three dominants to one recessive. The following table gives the actual figures and their proportions:

The Hybrids.	*Their Progeny.*				*Proportions.*
1. Round seeds	Round	5474	wrinkled	1850	2·96:1
2. Yellow albumen	Yellow	6022	green	2001	3·01:1
3. Coloured seed-coat	Coloured	705	white	224	3·15:1
4. Plain pods	Plain	882	constricted	299	2·95:1
5. Green unripe pods	Green	428	yellow	152	2·82:1
6. Axial flowers	Axial	651	terminal	207	3·14:1
7. Long stems	Long	787	short	277	2·84:1

This result raised the question: What are these hybrids' progeny? Are they hybrids again, like their parents, or true-breeding individuals, like their grandparents? They were bred from in their turn (self-fertilised, of course), and it was found that, of the dominants, two in every three were hybrids, like their parents, and one bred true, like its grandparent, while, of the recessives, all bred true, like their grandparent.

The following scheme may indicate this result more clearly:

	Dominants.			Recessives.
The hybrids' progeny =	3			1
	Hybrids.		Breeding True.	Breeding True.
=	2	:	1 :	1

The following table gives the experimental figures:

	Dominants.			Recessives.	
	Hybrids.	Breeding True.		Hybrids.	Breeding True.
Round seed ..	372	193	wrinkled seed	0	all
Yellow albumen	353	166	green albumen	0	all
Coloured seed-coat	64	36	white seed-coat	0	all
Plain pods ..	71	29	constricted pods	0	all
Green unripe pods	60	40	yellow unripe pods	0	all
Axial flowers ..	67	33	terminal flowers ..	0	all
Long stems ..	72	28	short stems ..	0	all

Among these results, three are to be noted specially, namely:

(*a*) In every case the hybrids' progeny consist of two groups.

(*b*) These two groups are to each other numerically in the ratio 3:1—the former being dominants, the latter recessives.

(*c*) Each two groups contains equal numbers of individuals which breed true.

In addition to these, Mendel made an experiment in which the parent plants differed in two and another in which they differed in three pairs of characters. In that in which the parents differed in two pairs of characters, one parent had round seeds with yellow albumen, the other wrinkled seeds with green albumen. One parent carried two of the characters already shown to be dominants, the other the corresponding recessives. As is to have been expected, their hybrids carried the two dominant characters; the corresponding recessives had disappeared. But, when the hybrids were bred from, their progeny consisted of four kinds, in numbers and proportions as set out in the following table:

	Round seed with Yellow albumen.		*Round seed with green albumen.*		*wrinkled seed with Yellow albumen.*		*wrinkled seed with green albumen.*
Numbers	315		108		101		32
Proportions	9	:	3	:	3	:	1

This again raised the question: Were the hybrids progeny hybrids or pure-breeding? To answer it their seeds were sown and, from the generation so produced, it was found, as in the previous experiment that some were hybrids, some bred true. The seeds carrying the two recessive characters (group 4) all bred true, but, of those carrying one or other of the dominants (groups 2 and 3), one in three bred true, while, of those carrying both the dominants (group 1), only one in nine bred true. This means that, since groups 2 and 3 contained three times as many and group 1 nine times as many seeds as group 4, each group contained equal numbers of true-breeding individuals. The following are the experimental figures:

	Round seed with Yellow albumen.	*Round seed with green albumen.*	*wrinkled seed with Yellow albumen.*	*wrinkled seed with green albumen.*
Bred from	301	102	96	30
Breeding true	38	35	28	30

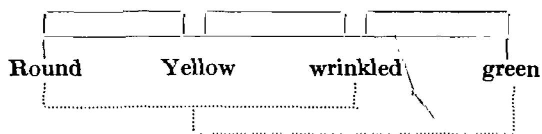
Among these results, three are again to be specially noted, namely:

(*a*) The hybrids' progeny consist of four groups.

(*b*) These four groups are to each other numerically in the proportion 9:3:3:1; and

(*c*) Each group contains equal numbers of true-breeding individuals.

But it is to be observed, in addition, that, since a dominant and its own recessive cannot both be carried by the same seed, the characters carried by the four groups together represent all the possible combinations of the four parental characters taken two at a time. This may be made clearer by the following diagram, in which the possible combinations are indicated by continuous, the impossible by dotted, lines:



In the experiment in which the parents differed in three pairs of characters, one had round seed, yellow albumen, and coloured seed-coat, the other had wrinkled seed, green albumen, and white seed-coat. The first parent carried three of the dominants dealt with in the first experiments, the other the three corresponding recessives. The result of the cross was 687 hybrid seeds, all of which were round, with yellow albumen and coloured seed-coat. From these 687 seeds, 639 plants were grown which were found to consist of eight different kinds, with seeds bearing the characters named in the following table, and standing to each other numerically in the proportion indicated.

	Round Yellow Colrd.	*Round Yellow white.*	*Round green Colrd.*	*wrinkled Yellow Colrd.*	*Round green white.*	*wrinkled Yellow white.*	*wrinkled green Colrd.*	*wrinkled green white.*
Numbers	269	98	86	88	27	34	30	7
Proportions ..	27 :	9 :	9 :	9 :	3 :	3 :	3 :	1

These 639 plants were all bred from, and it was found that, though they consisted of eight different groups, each group contained equal numbers of true-breeding individuals. The following are the figures:

Round Yellow Colrd.	*Round Yellow white.*	*Round green Colrd.*	*wrnkld. Yellow Colrd.*	*Round green white.*	*wrnkld. Yellow white.*	*wrnkld. green Colrd.*	*wrnkld. green white.*
8	14	9	8	11	10	10	7

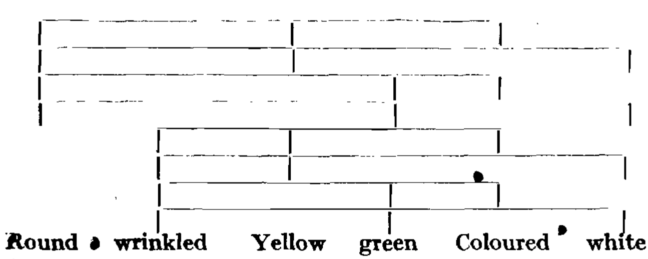
Among these results, four are to be noted specially, namely:

(*a*) The hybrids' progeny consist of eight groups.

(*b*) These eight groups are to each other numerically in the ratio 27:9:9:9:3:3:3:1.

(*c*) Each group contains equal numbers of true-breeding individuals; and

(*d*) The six parental characters are combined three at a time in all the possible combinations in which, because dominants cannot combine with their own recessives, they can be combined. This may be made clearer by the following diagram, in which only the possible combinations are indicated:



Having described his experiments so far in greater detail than need be considered here, Mendel proceeds: "Besides these, further experiments were made, with a smaller number of experimental plants, in which the remaining characters were combined in two-pair and three-pair hybrids, and all produced approximately the same result. There can be no doubt, therefore, that, for all the characters dealt with in the experiments, it can be said with certainty that the progeny of the hybrids in which several essentially different characters are united are the members of a combination series in which the ratios for every pair of differentiating characters are combined.[1] Thus, at the same time, it is evident that the behaviour of every pair of differentiating characters united in hybridising is independent of the other differences between the two parent plants."

This means that, if hybrids are produced from parents differing in, say, two pairs of characters, their progeny form a series which is found by multiplying the numerical ratio of one pair by that of the other, thus (using Mendel's experiment in which round peas with yellow albumen were crossed by wrinkled peas with green albumen, and putting their initial letters for the different characters):

3 Y+1 g
3 R+1 w
9 RY+3 Rg+3 Yw+1 wg.

If the parents differ in a third pair of characters, their hybrids form a series which is found by multiplying the series formed by the two first pairs by the ratio for the third, thus (putting C for coloured seed-coat and c for colourless):

[1] Stellen sie Glieder einer Combinationsreihe vor, in welchem die Entwicklungsreihe für je zwei differirende Merkmale verbunden sint.

9 RY+3 Rg+3 wY+1 wg
3 C+1 c

27 RYC+9 RgC+9 wYC+3 wgC+9 RYc+3 Rgc+3 wYc+1 wgc

And so on, for any number of pairs.

How this distribution is brought about may be indicated in another way. The first pair of characters divides the hybrids' progeny into two groups in the proportion 3 dominants to 1 recessive. The second pair subdivides each of these two groups in similar proportions. But, if the first recessive group is to be divided into two groups in the proportion 3 : 1, it must contain at least 4 individuals; and if the recessive group contain 4 individuals, its dominant must contain three times as many, *i.e.* 12. Thus the action of the second pair of characters is to divide a group of 4 into two groups of 3 and 1, and a group of 12 into two groups of 9 and 3; and so on, for any number of pairs of characters, as indicated in the following scheme:

R				:	w			
3				:	1			
RY		:	Rg	:	wY	:	wg	
9		:	3	:	3	:	1	
RYC	RYc		RgC	Rgc	wYC	wYc	wgC	wgc
27 :	9 :		9 :	3 :	9 :	3 :	3 :	1

And, as Mendel points out, this regular distribution of the characters would not occur, if the distribution of any one pair were interfered with by that of any other.

II

MENDEL'S LAW

THE result of Mendel's experiments was to show that hybrids do not breed erratically, as had been believed hitherto, but with extraordinary regularity, as is made clear by the observations insisted upon in the previous chapter, namely:

(*a*) When the original parents differ in one pair of characters, their hybrids' progeny are of two kinds, but the number of kinds or groups in the hybrids' progeny is doubled with every additional pair of characters in which the original parents differed.

(*b*) The number of individuals in the several groups or kinds can be arranged in the series $(3-1)^n$, where n stands for the number of pairs in which the original parents differed.

(*c*) The characters borne by all the groups in a set together represent all the possible combinations in which the differentiating parental characters can be combined.

(*d*) Each group in a set of hybrids' progeny contains equal numbers of constant or true-breeding individuals.

It now became Mendel's task to discover the law which produces this regularity and formulate it in words; and this he did in the following statement: "The results of these experiments caused further experiments to be made which appeared capable of furnishing information as to the nature of the egg and pollen cells of the hybrids. The occurrence, among the pea hybrids' progeny, of constant forms, and these even in all the possible combinations of the combined characters, gives an important clue. So far as experience goes, we find it universally true that constant progeny can be produced only when the egg cells and the fertilising pollen are of like kinds: that is when both are furnished with the materials[1] to produce completely like individuals, as happens in the normal fertilisation of pure kinds. We must, therefore, conclude that completely like factors co-operate in the production of constant forms among the hybrid plants. Since the various constant forms are produced not only on a single plant, but even on a single flower of that plant, the assumption seems sound that, in the ovaries of the hybrids, as many kinds of egg cells, and, in the anthers, as many kinds of pollen cells are formed as there are combination forms possible, and that, in their internal constitution, these egg and pollen cells correspond with the different forms.[2]

"In fact, it could be shown theoretically that, on these assumptions, the behaviour of the hybrids in individual generations would be explained completely, if it could be assumed, at the same time, that the different kinds of egg and pollen cells are formed in the hybrids in equal numbers, on the average."

Mendel's argument might, perhaps, be simplified, if broken up into these four propositions, the first three of which are mere statements of fact, with deductions which are obvious, while the fourth is his hypothesis to account for the hybrids' behaviour:

1. Pure species produce constant or true-breeding forms, and, consequently, must be furnished with the materials for doing so.

2. Hybrids also produce true-breeding forms, and

[1] Anlage. [2] Ihrer innern Beschaffenheit nach.

therefore must also be furnished with the materials for doing so.

3. Hybrids produce true-breeding forms in all the combinations in which the characters carried by their parents can be combined, and therefore must be furnished with all the materials to produce all these true-breeding forms.

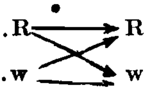
4. Hybrids produce equal numbers of these true-breeding forms, and must, therefore, be furnished with equal numbers of the materials for their production.

Mendel remarked that, if his theory were assumed to be correct, the behaviour of hybrids could be explained "theoretically," but did not stop to make this explanation. Meantime, it will be well to consider how it might have been made, before proceeding to consider his experiments to prove that hybrids are furnished with equal numbers of the materials to produce their progeny's—and to reproduce their parents'—characters.

Consider, first, the case in which the parents differ in one pair of characters: in one having round while the other has wrinkled seed. The theory is that, in their hybrids, both the ovaries and the anthers contain equal numbers of the materials for the production of both roundness and wrinkledness. If the materials be represented by the initial letters of the characters they produce, with capitals for dominants and small letters for recessives, the following scheme should represent their distribution in the hybrids:

In the Ovaries.	*In the Anthers.*
......................R	R......................
......................w	w......................

Since there are two kinds of materials in both ovaries and anthers, and one or other kind in one must unite with one or other kind in the other, the chances are even that R in the ovaries will unite with either R or w in the anthers, or that w in the ovaries will unite with either R or w in the anthers, and that one or other of the four combinations RR, Rw, wR, ww will be formed. A diagram may make this clearer:



Rw and wR being the same, the chances are 1 : 2 : 1 that RR or Rw or ww will be formed, or, if sufficient fertilisations be made, that the combinations formed should be 1 RR : 2 Rw : 1 ww. But, since the progeny receiving the materials RR and Rw are round, while those receiving ww are wrinkled, the chances are that three round seeds are produced for one wrinkled; and, since the progeny receiving the materials RR receive one kind of materials only, while those receiving the materials Rw receive two, the chances are that only one in every three round seeds shall breed true. At the same time, all the progeny receiving the materials ww should breed true. Thus, Mendel's hypothesis is consistent with the phenomena observed in his experiments.

Consider, next, the case in which the parents differ in two pairs of characters: in one having round seed with yellow albumen, while the other has wrinkled seed with green albumen. According to the hypothesis, the materials offered should be:

In the Ovaries.	*In the Anthers.*
R	R
w	w
Y	Y
g	g

The chances are that equal numbers of the combinations RR, Rw, wR and ww, and of the combinations

YY, Yg, gY and gg should be formed. But, since the two sets of materials are distributed independently, the combinations formed by the one set should be distributed equally among the combinations formed by the other. For instance, among the seeds carrying the materials RR, equal numbers should be found carrying the materials YY, Yg, gY, and gg, and so on for the other combinations in which R and w are concerned. This may be made clearer by the following diagram, in which the distribution of the R and w materials is indicated horizontally, that of the Y and g materials perpendicularly:

RR YY	Rw YY	wR YY	ww YY
RR Yg	Rw Yg	wR Yg	ww Yg
RR gY	Rw gY	wR gY	ww gY
RR gg	Rw gg	wR gg	ww gg

If this diagram be examined, it will be seen that, if sixteen seeds are produced, there should be 9 round with yellow albumen, 3 round with green albumen, 3 wrinkled with yellow albumen, and 1 wrinkled with green albumen, and, further, that there should be only one seed pure for both parental characters in each of these groups. The pure seeds are indicated by circles. Thus, again, Mendel's hypothesis is consistent with the observed phenomena.

The case in which the original parents differed in three pairs of characters could be illustrated similarly, but the diagram becomes tri-dimentional and, therefore, over-complicated.

Thus, if it be assumed that the hybrids are furnished with equal numbers of the materials to produce their parents' characters, Mendel's theory can be shown to be true: can be proved "theoretically."

To prove it experimentally—to prove that hybrids are furnished with equal numbers of reproductive materials—Mendel had more hybrids bred like those previously bred between parents differing in two pairs of characters: that is between parents having round seeds with yellow albumen and others having wrinkled seeds with green albumen. The earlier experiments had shown that such hybrids were furnished with the materials for the production of round seeds and wrinkled seeds, seeds with yellow albumen and seeds with green albumen. Mendel's task was now to show that they contained these materials in equal numbers. The hybrids were mated with both their pure-breeding parents twice: the hybrids being the pollen-bearers in one mating, the parents in the other, thus:

Experiment.	*Egg-Bearers.*	*Pollen-Bearers.*
1.	The hybrids.	Parents with Round seeds and Yellow albumen.
2.	The hybrids.	Parents with wrinkled seeds and green albumen.
3.	Parents with Round seeds and Yellow albumen.	The hybrids.
4.	Parents with wrinkled seeds and green albumen.	The hybrids.

According to previous experiments, the materials offered by the hybrids and their recessive parental kind in experiments 2 and 4 are represented by the following scheme:

By the Hybrids.	*By the Recessive Parental Kind.*
......................R	w......................
......................w	w......................
......................Y	g......................
......................g	g......................

If the hybrids are furnished with equal numbers of the materials R and w on the one hand, and Y and g on the other, then equal numbers should be produced of the combinations Rw and ww on the one hand, and Yg and gg on the other. But, since the two sets of materials are distributed independently, the two combinations formed by the one set should be distributed evenly among the two formed by the other, thus:

Rw → Yg gg　　　ww → Yg gg

And the progeny of the hybrids and their recessive parental kind should consist of four kinds, equal in number, namely:

Carrying the materials	Rw Yg	Rw gg	ww Yg	ww gg
Showing the characters	Round seeds with Yellow albumen	Round seeds with green albumen	wrinkled seeds with Yellow albumen	wrinkled seeds with green albumen
	1 :	1 :	1 :	1

The numbers actually produced were:

	Round seeds with Yellow albumen.	*Round seeds with green albumen.*	*wrinkled seeds with Yellow albumen.*	*wrinkled seeds with green albumen.*
With the parents as pollen-bearers ..	31	26	27	26
With the hybrids as pollen-bearers ..	24	25	22	27

According to previous experiments, the materials offered by the hybrids and their dominant parental kind, in experiments 1 and 3, are represented by the following scheme:

By the Hybrids.	*By the Dominant Parental Kind.*
......................R	R......................
......................w	R......................
......................Y	Y......................
......................g	Y......................

If the hybrids are furnished with equal numbers of the materials R and w on the one hand, and Y and g on the other, then equal numbers should be produced of the combinations RR and Rw on the one hand, and YY and Yg on the other. But, since the two sets of materials are distributed independently, the two combinations formed by the one set should be distributed evenly among the two formed by the other, thus:

RR		Rw	
YY	Yg	YY	Yg

and the progeny of the hybrids and their dominant parent kind should consist of four kinds, equal in number, namely:

Carrying the materials	RR YY	RR Yg	Rw YY	Rw Yg
Showing the characters	Round seeds with Yellow albumen	Round seeds with Yellow albumen	Round seeds with Yellow albumen	Round seeds with Yellow albumen
	1 :	1 :	1 :	1

The numbers actually produced were:

	Round Seeds with Yellow Albumen.
With the parents as pollen-bearers	98
With the hybrids as pollen-bearers	94

The seeds bred in these four experiments were all, in outward appearance, as the theory had predicted, and so might be taken as giving sufficient evidence that the theory is sound. But Mendel did not take them as giving such evidence. He took them as giving presumptive evidence only, and made further experiments. The seeds gave evidence through their external characters only. Mendel decided they should also give evidence through the materials with which they were furnished, and so bred from them again and produced another generation. On looking back to page 17, it will be seen that, in experiments 2 and 4, the first group of the hybrids' and their recessive parents' progeny should be hybrid in both sets of materials, the second in those for shape only, the third in those for colour of albumen only, the fourth pure in both sets. They should carry the materials set down below and, in the next generation, produce seeds of the kinds set down below again:

	Group 1.	*Group* 2.	*Group* 3.	*Group* 4.
Should carry materials	Rw Yg	Rw gg	ww Yg	ww gg
Should produce	Round and Yellow.			
	Round and green.	Round and green.		
	wrinkled and Yellow.		wrinkled and Yellow.	
	wrinkled and green.	wrinkled and green.	wrinkled and green.	wrinkled and green.

Each group produced only the kinds of seeds the theory demanded.

On looking back to page 18, it will be seen that, in experiments 1 and 3, though all the progeny of the hybrids and their dominant parent should have round seeds with yellow albumen, only the first group should be pure in both kinds of materials, while the second should be hybrid in those for colour of albumen, the third in those for shape, and the fourth in both kinds. They should carry the materials set down below and, in the next generation, produce seeds of the kinds set down below again:

	Group 1.	*Group* 2.	*Group* 3.	*Group* 4.
Should carry materials	RR YY	RR Yg	Rw YY	Rw Yg
Should produce	Round and Yellow.	Round and Yellow. Round and green.	Round and Yellow. wrinkled and Yellow.	Round and Yellow. Round and green. wrinkled and Yellow. wrinkled and green.

When they were bred from and their progeny examined, the following were the numbers belonging to each of these groups:

	Group 1.	*Group* 2.	*Group* 3.	*Group* 4.
With the pure parents as pollen-bearers ..	20	23	25	22[1]
With the hybrids as pollen-bearers ..	25	19	22	21[2]

Again there were four groups of seeds equal in number and producing only the kinds of seeds the theory demanded.

In Mendel's final experiment to prove his theory, a hybrid in one pair of characters: violet-red flowers and white, the former the dominant: was mated with

[1] Eight of the 98 seeds produced in the previous germinations failed to grow and reproduce.

[2] Seven of the 94 seeds produced in the previous germinations failed to grow and reproduce.

a hybrid in another pair: long stem and short, the former the dominant. The first-named hybrid had short stems, the last white flowers. The materials offered by the two hybrids should be, putting V for violet-red, w for white, L for long, and s for short, as indicated in the following scheme:

By One Hybrid.	*By the Other Hybrid.*
......................V	w......................
......................w	w......................
......................s	L......................
......................s	s......................

If the hybrids are furnished with equal numbers of the parental differentiating materials, equal numbers of the combinations Vw and ww should be produced on the one hand, and Ls and ss on the other. But, since the materials are distributed independently, the two combinations formed by one set should be distributed equally among those formed by the other, thus:

Vw — Ls, ss   ww — Ls, ss

and the progeny of the two hybrids should consist of four kinds, equal in number, namely:

Carrying the materials	Vw Ls	Vw ss	ww Ls	ww ss
Showing the characters	Violet-red flowers and Long stems.	Violet-red flowers and short stems.	white flowers and Long stems.	white flowers and short stems.

The numbers actually produced were:

Violet-red with Long stems.	*Violet-Red with short stems.*	*white with Long stems.*	*white with short stems.*
47	38	40	41

Again there were four groups of plants in numbers and kinds as the theory demanded.

Thus Mendel's theory that hybrids are furnished with equal numbers of the materials to produce their parents' characters is proved experimentally and becomes a law.

NOTE.—It will have been noticed that none of Mendel's experimental results is in *exact* accordance with the theory. In none of the experiments were the hybrids' progeny in the exact proportions 3 : 1, or 9 : 3 : 3 : 1, and so on; nor were the true-breeding individuals in any number of groups in *exactly* equal numbers. This, as Mendel well knew, could not be expected, unless he bred an extraordinarily large number of plants. But he also knew that, if his figures came out with approximate accuracy, time after time, when smaller numbers were bred, theoretical accuracy would be attained if sufficient numbers were bred. He satisfied himself, and should satisfy anybody else, on this point, by breeding unusually large numbers in his experiments with the two pairs of characters round and wrinkled seeds and yellow and green albumen, and getting ratios so close to the theoretical that it can be assumed, without any doubt, that, if similarly large numbers had been bred, in the remaining experiments, the experimental and the theoretical ratios would have been in equally close agreement. The figures and ratios in these two experiments are a good illustration of how experimental and theoretical results agree as numbers are increased:

	Dominants Produced.		*Recessives Produced.*	*Dominants which were Hybrids.*		*Dominants which Bred True.*
Numbers	5474		1850	372		193
	6022		2001	353		166
Ratios	2·96	:	1	1·93	:	1
	3·01	:	1	2·12	:	1

III.

OBSERVATIONS AND DEDUCTIONS

IN order to facilitate future work, it will be useful to set down a few observations and simple deductions from Mendel's experiments. Some may seem very obvious, some even trivial, but all may be useful.

1. If the original parents differ in n pairs of characters, their hybrids' progeny consist of 2^n groups, the numbers in which are to each other in the ratio $(3:1)^n$, thus:

Pairs of Differing Characters.	*Number of Groups.*	*Ratio.*
1	2	3 : 1
2	4	9 : 3 : 3 : 1
3	8	27 : 9 : 9 : 9 : 3 : 3 : 3 : 1
.	.	.
.	.	.
.	.	.
n	2^n	$(3 : 1)^n$

2. Conversely, if the hybrids' progeny consist of 2, 4, 8, 16 . . . 2^n groups, the numbers in which are in the ratio $(3 : 1)^n$, then the parents differed in 1, 2, 3, 4 . . . n pairs of characters.

3. As the pairs of characters in which the original parents differ increase, the total number of groups increases, the number of individuals in the largest group increases, and the numbers of equal-sized groups increase; but no more individuals in each group breed true in all their characters, thus:

	Number of Groups when the Parents Differ.					
Containing.	*In 1 Pair.*	*In 2 Pairs.*	*In 3 Pairs.*	*In 4 Pairs.*	*In 5 Pairs.*	*Containing Individuals Breeding True.*
1 individual	1	1	1	1	1	1
3 individuals	1	2	3	4	5	1
9 ,,		1	3	6	10	1
27 ,,			1	4	10	1
81 ,,				1	5	1
243 ,,					1	1
Total	2	4	8	16	32	

For example, when the parents differ in three pairs of characters, there are eight groups of hybrids' progeny: one containing 27 individuals, three containing 9 each, three containing 3 each, and one containing 1; but, in each of these groups, only *one* individual breeds true in all its characters.

4. Since two of the groups in the hybrids' progeny are like the original parents, the number of new kinds produced in any set of hybrids' progeny is two less than the number of groups in the set, thus:

Differentiating Parental Pairs of Characters.	*Groups in the Hybrids' Progeny.*	*New Kinds.*
1	2	0
2	4	2
3	8	6
4	16	14
.	.	.
.	.	.
.	.	.
n	2^n	$2^n - 2$

5. The hybrids carry all the dominant characters carried by the original parents, and, if the recessives of the individual dominants can be identified, at the

hybrid generation, the breeding behaviour of the hybrids can be predicted.

6. In a set of hybrids' progeny, the largest group carries all the dominants, the next-sized groups one less, the next-sized groups again two less, and so on down to the smallest group, which carries all the recessives. Compare as examples the following two- and three-pair sets:

X	X	x	x
Y	y	Y	y

9 XY : 3 Xy : 3 xY : 1 xy

X	X	X	x	X	x	x	x
Y	Y	y	Y	y	Y	y	y
Z	z	Z	Z	z	z	Z	z

27 XYZ : 9 XYz : 9 XyZ : 9 xYZ : 3 Xyz : 3 xYz : 3 xyZ : 1 xyz

7. In a two-pair set, the first group differs from the next two groups each in one pair of characters, from the last in two pairs; the two middle groups differ from each other in two pairs of characters, and from the last in one.

8. Each character in which the *original* parents differed is carried by half the groups in their hybrids' progeny. For example, in the two-pair set of four groups above, two groups carry X, 2 Y, 2 x, and 2 z; in the three-pair set four groups carry X, 4 x, 4 Y, 4 y, 4 Z, and 4 z.

9. The remaining characters carried by a set of hybrids' progeny outside those in which the original parents differed are the same for all the progeny. This statement may seem too obvious, and therefore unnecessary, but, in the solution of some problems, it may be useful if put in particular forms, thus:

(*a*) If one or more groups in a set are found to carry a character outside those concerned in the production of the set, that character is common to all the groups in the set. If, for instance, the first group in the following two-pair set were found to carry Z', then, unless they also carried Z, the middle groups would differ from the first in more than one pair of characters.

9	XYZ
3	Xy
3	xY
1	xy

(*b*) If more than half the groups in a set carry a character not concerned in the production of the set, that character is carried by all the other groups in the set. If, for instance, the third group in the following two-pair set did not carry Z, it would differ from the first and last groups in more than one pair of characters and from the other middle group in more than two:

9	XYZ
3	XyZ
3	xY
1	xyZ

10. If two or more groups in the hybrids' progeny be inseparable, the number of groups will be one less than the normal for every group which is inseparable from another, and the number of individuals in one group will be the number in the inseparable groups together; for examples:

If the first two groups in a two-pair set be inseparable, there will apparently be only three groups, thus:

X	X	x	x
Y	y	Y	y
12		: 3 :	1

If the last two groups be inseparable, there will be only three apparent groups, thus:

X	X	x	x
Y	y	Y	y
9	3 :	4	

If the first three groups be inseparable, there will be only two apparent groups, thus:

X	X	x	x
Y	y	Y	y

15 : 1

If the last three groups be inseparable, there will be only two apparent groups, thus:

X	X	x	x
Y	y	Y	y

9 : 7

11. If hybrids are mated with their pure parental kinds, as many kinds are produced as are produced when the hybrids are mated with each other; but the numbers in each kind produced are equal. This is illustrated by Mendel's experiments.

12. It must not be assumed that every character finds another with which it forms a pair, for there may be—probably are—species, even genera, carrying characters which never vary.

It must be remembered that the foregoing observations and deductions hold only when the materials (*anlage* in the original German), which now may be called *factors*, for the production of characters are distributed normally. Since the finding of Mendel's papers, nothing has been discovered which would modify Mendel's law: that hybrids are furnished with equal numbers of the factors to produce their parents' characters: but it has been found that the factors are sometimes distributed abnormally, and that sometimes their effects are obscured, as, for instance, when (*a*) Two or more factors are tied, linked, or coupled together, and so handed on from generation to generation as one factor.

(*b*) One factor does not blot out its alternative factor's effect—*i.e.*, when one of a pair is not dominant to the other.

(*c*) One factor mates with another at one time, and with another still at another time—*i.e.*, when factors are polygamous.

(*d*) The effect of one factor is suppressed by that of another.

(*e*) The effect of one factor is indistinguishable from that of another.

(*f*) Two or more factors produce closely similar effects.

As what has been said so far should be a sufficient introduction to Mendelian work, when the factors are distributed normally and their effects are normal, we shall now give attention to examples in which the distribution of the factors or their effects is not normal, and, as our object is to make such abnormalities as clear as may be, we shall select such examples as suit best for this purpose, without regard to their importance from any other point of view. We shall also consider the simpler abnormalities first.

IV

WHEN NEITHER OF A PAIR OF FACTORS IS DOMINANT

British breeds of live stock had their origins usually in the union of two or more kinds, and therefore, in their early days, were impure in a greater or smaller number of their characters. But, preferring certain characters, breeders bred from animals bearing the preferred, discarded animals bearing other characters, and so made their breeds purer and purer in an ever-increasing number of characters. With recessive characters purity was obtained at once, but with dominant characters only gradually and slowly. Indeed, though many breeds are now more than a century old, it might be rash to say that any one is yet absolutely pure, not only in all, but even in one of its dominant characters.

In its early days, the Suffolk breed of horses was of several colours, but, since the breeders decided to have chestnut only and bred only from chestnuts, the breed has had no other colour. In their early days, there were black cattle and cattle of other colours in the parts of England which now have red breeds of cattle; but, so soon as the breeders decided to have red only and bred only from red cattle, their breeds have had no other colour.

It was otherwise, however, when the characters the breeders preferred their stock should carry happened to be dominants. Breeders of black cattle bred from black parents only, but sometimes a red calf appeared;

breeders of hornless cattle would breed from hornless parents only, but sometimes a calf would appear with scurs (*i.e.*, the outer horn covering), or with the horn core, or, less often, with both core and covering; and horse breeders with a dislike to chestnut in some breeds, or to black in others, or to both in others, would avoid parents of these colours; yet chestnut or black foals sometimes appeared. As time went on, however, and breeders persisted in breeding from parents carrying the desired dominant characters only, the numbers of young born with the undesired recessive characters grew smaller and smaller. Obviously, with time and persistence, the desired dominant characters would eventually breed true.

But there are characters which, even with time and persistence, never will breed true. The first known of these is the colour of the Blue Andalusian fowl, which was described by Professor Bateson thus:

"Andalusians are in general colour what fanciers call blue—namely, a diluted black. In the cocks the hackles and saddle feathers are full black, and the feathers of the breast are edged or 'laced' with black. The hens are blue, laced with black more or less, all over. This breed is recognised by the fanciers as never breeding true to colour. When blue is bred with blue, three colours are produced, blacks, blues, and a peculiar white splashed with grey."

In 1902, Professors Bateson and Punnett learned from a breeder of Andalusians that her blue birds of that year had thrown 36 blue birds, 22 blacks, and 17 whites. Professors Bateson and Punnett obtained and bred from birds of all three kinds and found that:

(*a*) Blue x blue threw 42 blue birds, 19 blacks, and 22 whites.

(*b*) Black x black bred true.

(*c*) White x white bred true; and

(*d*) Black x white threw Blue Andalusians.

Obviously, Andalusian blue is the hybrid between black and "white splashed with grey," but, unlike Mendel's seven original hybrids, is like neither parent. It is intermediate between the two; thus neither parent is dominant. But, when bred with itself or with its parent kinds, it behaves like the hybrids between the seven original pairs, thus:

	Hybrids.		*Blacks Breeding True.*		*Whites Breeding True.*
Hybrid x hybrid produces	78		41		39
I.e.,	2	:	1	:	1

	Hybrids.		*Blacks.*
Hybrid x black produces	27		19
I.e.,	1	:	1

	Hybrids.		*Whites.*
Hybrid x white produces	34		20
I.e.,	1	:	1

But for the absence of dominance, these two colours and their hybrids behave in the ordinary Mendelian manner.

Among European cattle there are at least five true-breeding colours, each of which may be of many different shades, or, at any rate, may carry the factors for different shades; and most of the hybrids between these five colours are intermediate or perpetual hybrids. The colours and their progeny are indicated in the following scheme, in which the pure progeny are printed in capital type, the Mendelian hybrids in ordinary type, and the intermediate hybrids in italics:

		Pure-breeding Parents				
		Black	Red	Light or steel dun	Brown	White
				Progeny		
Pure-breeding parents.	Black	BLACK	black	*ordinary dun*	*black brindle*	*blue roan*
	Red		RED	*yellow*	*red brindle*	*red roan*
	Light or steel dun			LIGHT DUN	*light brindle*	(?)
	Brown				BROWN	(?)
	White					WHITE

In Britain there are four or five black and as many red breeds, but no breed containing only light duns, or browns, or whites. But light duns and browns are found among Highlanders, browns and, possibly, light duns among Jerseys, browns among Ayrshires and Longhorns, and whites among Shorthorns. Some coloured breeds and animals, as, for instance, the Dutch, the Ayrshire, the Hereford, and the red-and-white Shorthorns, have larger or smaller portions and patches of their bodies without colour, and, occasionally, an animal with an extremely small coloured area is misdescribed as white. Though it would be very difficult to find another adjective to describe them, the "wild white" cattle of Britain and the so-called "white" cattle of eastern and southern Europe are not white, but really blacks or reds carrying factors which prevent the production of pigment elsewhere than about the ears, and round the eyes and muzzle. They sometimes throw black or red calves, according as they carry black or red pigment. The white Shorthorn, on the other hand, is a whole white which throws white calves only.

Of these perpetual hybrid colours, the red roan, which is found among Shorthorns, has received most attention. The Shorthorn's ancestors were brought over from the Low Countries to Lincolnshire, Yorkshire, and Durham in the seventeenth and eighteenth centuries. The bulk of them were red-and-white, but there must have been white ones imported also, for there were no whites of the same kind in the country before, and a few whites are reported in parts of the country occupied by the red-and-whites in the first half of the eighteenth century.[1] Besides, there was a herd of these white cattle at Studley Royal, in Yorkshire, in the middle of the eighteenth century, to which early breeders of the imported cattle turned for breeding stock. Roans were recorded among their descendants—among the descendants of red-and-whites and whites—about 1770, and, when their stock were well enough established to be called a breed in the beginning of the nineteenth century, the breeders described their colours as red, white, and roan.

As time went on, the breeders developed a preference for reds and roans—sometimes the one colour being more highly favoured, sometimes the other—and a corresponding dislike for whites. Consequently, whites were less often bred from; yet whites persisted in being born in little or no less numbers. The breeders found that the whites were thrown by roans, and, arguing that the roans must still be affected by the original or some less remote white cross, tried to have their roans breeding true by breeding from such as had no whites in their nearer ancestry. Still the roans threw whites. They threw reds also, but reds were welcomed, and, when they threw them, the roans were not accused of having a

[1] It is possible that the white Shorthorn and the white Charolais cattle are descended from the same stock.

"reversionary taint," as they were when they threw whites.

The first set of data dealing with the subject was extracted from volumes 37 to 49 of Coates's—*i.e.*, Shorthorn—"Herd Book" by Professor Karl Pearson and Miss Barrington and published in *Biometrica* in 1906. These writers wished to show that Shorthorn colours are inherited in the Galtonian, not in the Mendelian, manner. For their purpose, the colours were arranged in five groups, namely, red, red-and-white, red-and-little-white, roan, and white. So arranged, the data gave no very strong support for either manner of inheritance, but, when the three red groups were lumped into one, the evidence in favour of the Mendelian manner became not only highly presumptive, but capable of being strengthened. The first half of the following table shows the proportions in which the three colours should have been produced by all the possible matings, if red and white be true-breeding colours and roan their intermediate hybrid; the second half shows the actual numbers produced according to Professor Pearson's and Miss Barrington's data. The discrepancies are enclosed within brackets.

	Should have been Produced.			*Produced.*		
Matings.	*Roan.*	*Red.*	*White.*	*Roan.*	*Red.*	*White.*
Red x red	—	all	—	(25)	413	—
White x white	—	—	all	—	—	3
Red x white	all	—	—	128	(7)	—
Roan x roan	2 :	1 :	1	278	152	84
Roan x red	1 :	1	—	521	483	(4)
Roan x white	1 :	— :	1	47	(3)	24

But the origin of the data must be examined before any conclusion is to be drawn from them. They are not experimental figures. The observations behind them were not made by experimenters, but by stock-owners who described their animals, generally when they were young, so that they could be identified again at any time by the owner or any other breeder. Lacking the experimenter's motive for absolute accuracy, the breeder may be accurate enough for his purpose, but not for the experimenter's. The breeder's chief inaccuracy is misdescription. A red may be described as a roan, a roan as a red. The roan coat is a mixture of red hairs and white in varying proportions on different animals. When the white hairs are few, they may not be seen by the breeder, unless looked for with care, and the animal carrying them is misdescribed as red. The white hairs of a roan animal may, perhaps, be seen most readily, where the coat is shortest, below the tail. Red animals vary from whole red to very nearly white. When the white flecks are large or well defined, the chances of misdescription are less, but, when they are small and numerous, more especially when the margins between the red and the white flecks are ragged and irregular, a red may be described as a roan. The first line in Professor Pearson's and Miss Barrington's table is evidence that red and roan Shorthorns are misdescribed, for, if not, why should 438 red x red matings produce 25 roans, when all other red cattle, pedigreed and non-pedigreed, breed true? The reasons for the varying proportions of white hairs to red are not known, but there is some indication that the degree of white in the mixture and the degree of flecking are related. In crosses between whole-coloured black Galloways or Aberdeen-Angus and white Shorthorns the white hairs are usually few, while in crosses between the highly flecked Ayrshire and white Shorthorns they are usually many.

Besides misdescriptions, herd-book records are liable to other errors. Calves of unwanted colours or with unwanted characters of other kinds may not be registered at all. Registration would not increase their own value, and might advertise one or both their parents' weakness. When there are more than one sire in a herd, a calf's paternity may be attributed wrongly, and, unfortunately, the substitution of one calf for another has not been entirely unknown.

The wrong colours—those within brackets—in Professor Pearson's and Miss Barrington's table may be accounted for by the breeder's errors of description, and the shortage of white calves in the roan x roan and roan x white matings by his antipathy to whites.

In 1908, in the hope of getting data which might be less affected by these errors, the present writer collected from volume 52 of Coates's "Herd Book" (published in November, 1906) all the entries made by a number of breeders who, because of the value of their cattle, might be expected to register most of them, and would not be suspected of substituting one calf for another.[1] The following table is the result:

	Roan.	*Red.*	*White.*
Red x red produced	(5)	90	—
White x white produced	—	—	1
Red x white produced	78	—	—
Roan x roan produced	178	90	102
Roan x red produced	209	214	(3)
Roan x white produced	34	—	19

This table is a little more satisfactory than the previous, because it contains a smaller proportion of wrong colours and because the proportions in which the different colours are produced by the last four matings are almost

[1] *Sci Proc. Royal Dublin Society,* vol. xi. (N.S.), No. 28.

as they should be, if roan be the hybrid between the two true-breeding colours red and white.

Still more satisfactory has been the evidence got by examining the "exceptions" reported since the 1908 paper was published. It has not been possible to have all the reported exceptions examined by competent examiners, because some were too far from examiners, some even in other countries, but, wherever they have been examined, the exceptions have been found to be themselves misdescribed or the progeny of one or two misdescribed parents. The two following examples may be taken as typical:—A breeder reported that his red sire was throwing white calves. On close examination, the sire, which had been described as red by his breeder, and seemed to be red, even when near, turned out to be a roan. Another breeder reported that his white sire was throwing no white calves. It was half-expected that the sire might be a roan, but the examiner found him white, without doubt, and all his calves of the year roans. But the dams of his calves of that year, as was found from the Herd Book, were all reds. He had not been given the chance of breeding a white.

V

INSEPARABLE OR COMBINED EFFECTS

An early example of the difficulty of separating the effect of one factor from that of another occurred in Professors Bateson and Punnett's experiments on the inheritance of fowls' combs. The experiments are detailed in the second and third "Reports to the Evolution Committee of the Royal Society," and summarised in the fourth.

When rose-combed fowl were mated with single-combed fowl, the hybrids had all rose combs. Thus, rose comb seemed dominant to single; and, when the hybrids were mated with each other, this inference was confirmed, for their progeny's combs were roses and singles in the proportion 3 : 1—actually 695 roses and 235 singles.

But pea comb seemed also dominant to single comb, for, when pea-combed and single-combed fowl were mated, their hybrids had all pea combs, and, when the hybrids were mated with each other, their progeny were peas and singles in the proportion 3 : 1—actually 567 peas and 210 singles.

Two dominants to one and the same recessive, one recessive to two dominants, was something new. Nothing like it had been seen in Mendel's experiments, in which each dominant had only one recessive and each recessive only one dominant. Then, if the factor for single comb be polygamous, so also, in all probability, are those for rose comb and pea comb. Rose and pea were mated, to discover which was the dominant, and it was found that neither was dominant, for their hybrids were neither rose combs nor pea combs, but a new kind different from both, shaped like a half-walnut.

This was another new phenomenon, but the significance of both phenomena was indicated, when the hybrid walnut combs were mated, for their progeny consisted of four kinds: walnuts, roses, peas, and singles: in the proportion 9:3:3:1—actually 279 walnut combs, 99 roses, 132 peas, and 45 singles. But, by observation 2,[1] four groups in the hybrids' progeny means two pairs of factors operating and two characters carried by the parental and each of the other three groups. And, since neither the two characters combining to make up walnut, or rose, or pea, or *single, nor the two factors* which produce them, can be identified and separated, all that can be done, meantime, is to represent the two-pair set of hybrids' progeny—walnut, rose, pea, and single—by "unknowns," thus:

Walnut.		*Rose.*		*Pea.*		*Single.*
X		X		x		x
Y		y		Y		y
9	:	3	:	3	:	1

The dominance of both rose and pea to single and the production of walnut by the mating of rose and pea can now be explained. Rose and pea each differs from single in one, but not the same, pair of characters. Both rose and single carry y, but rose carries X, while *single carries its recessive* x, and so rose is a simple dominant to single. Similarly, x is common to both pea and single, but pea carries Y, while single carries its recessive, y, and so pea is also a simple dominant to single. Again, rose carries the dominant X, pea the

[1] Page 39.

dominant Y, and, when they are mated, these two dominants are combined in their progeny, walnut.

A parallel example might be constructed from Mendel's peas. If round peas with green albumen be mated with wrinkled peas also with green albumen, their hybrids' progeny will consist of three round peas with green albumen to one wrinkled with green albumen; and if peas with yellow albumen but wrinkled skins be mated with peas with green albumen, but also wrinkled skins, their hybrids' progeny will consist of three with yellow albumen and wrinkled skins to one with green albumen and wrinkled skins; but, if peas with round skins and green albumen be mated with peas with yellow albumen and wrinkled skins, their hybrids will have round seeds with yellow albumen, and their hybrids' progeny will consist of:

Round Yellow.		*Round green.*		*wrinkled Yellow.*		*wrinkled. green.*
R		R		w		w
Y		g		Y		g
9	:	3	:	3	:	1

It may have been noticed that the numbers in the four groups of walnut combs' progeny were not too close to the 9 : 3 : 3 : 1 ratio. The actual numbers were 279, 99, 132, and 45. To some statisticians this discrepancy might seem serious, but the inference drawn from the actual figures was confirmed by other tests, one of which only need be mentioned. The hybrid walnut combs were mated with single combs. The materials offered should have been:

By the Walnuts.	*By the Singles.*
......................X	x......................
......................x	x......................
......................Y	y......................
......................y	y......................

which should have produced:

	X Y	X y	x Y	x y
	walnuts	roses	peas	singles
	1 :	1 :	1 :	1
There were actually produced ..	644	705	664	716

Another example of the difficulty of separating some individual causes and effects is to be found in Miss Durham's experiments on the colours of mice, the details of which are to be found in the fourth "Report to the Evolution Committee" and in the first volume of the *Journal of Genetics*. In Miss Durham's first experiment, agouti-coloured mice were mated with chocolates, and, while their hybrids were all agoutis, the hybrids' progeny were agoutis, cinnamon agoutis, blacks and chocolates in the proportion 9 : 3 : 3 : 1. Thus there are four groups and two pairs of factors and characters. Agouti carries the two dominant characters, chocolate the two recessives, while the others carry each one dominant and one recessive; but, since none of the two characters carried by any group can be separated, the set must be written down with "unknown" symbols, thus:

Agouti	XY	9
Cinnamon agouti	Xy	3
Black	xY	3
Chocolate	xy	1

In Miss Durham's next experiment, black was mated with a new colour, silver fawn, whose ability to mate with black proves the existence of one other factor at least. But their hybrids' progeny, which consisted of blacks, blues, chocolates, and silver fawn, in the ratio 9 : 3 : 3 : 1, showed that there was another pair of factors operating. Since it is the largest group, black, must carry two dominants. One may be Y, which the first experiment showed it to carry; the other a new factor, say Z. Nay, both may be new; and if they be called Z and A, then the characters carried by the four groups should be:

Black	ZA
Blue	Za
Chocolate	zA
Silver fawn	za

In that case, the characters carried by black and chocolate, as indicated by the two experiments, should be:

Black	xYZA
Chocolate	xyzA

But then black and chocolate would differ in two pairs of characters, whereas both experiments show them to differ in one only. Black carries only one new dominant, therefore, and if it be called Z, the characters now known to be carried by black are xYZ. At the same time, chocolate must also carry Z, for by the first experiment it already carries xy, and if it did not carry Z, it would differ from black in more than one pair of characters.

Since Y and Z and their recessives y and z are the characters combining to form the four groups in the second experiment, and black must carry both the dominants, silver fawn both the recessives, and chocolate has been shown to carry one dominant, Z, blue must carry the other dominant, Y, and, from both experiments, the characters now known to be carried by the four groups in the second experiment are:

Black	xYZ
Blue	Yz
Chocolate	xyZ
Silver fawn	yz

But because it is outside the characters combining to form the YZ set and is carried by black and chocolate, x must be carried by blue and chocolate also.[1]

The characters now known to be carried by the four groups in Miss Durham's first experiment are:

Agouti	XY
Cinnamon agouti	Xy
Black	x YZ
Chocolate	x y Z

But because it is outside the characters forming the XY set and is carried by black and chocolate, Z must also be carried by agouti and cinnamon agouti.

Since there are three pairs of factors operating, there must be eight groups in all, two of which remain to be found. Those already found and those remaining to be found are:

Agouti	XYZ	27
	XYz	9
Cinnamon agouti	XyZ	9
Black	xYZ	9
	Xyz	3
Blue	xYz	3
Chocolate	xyZ	3
Silver fawn	xyz	1

In Miss Durham's third experiment, agouti was mated with blue, and the hybrids' progeny were agoutis, dilute agoutis, blacks, and blues, in the proportion 9 : 3 : 3 : 1. The characters carried by three of these groups are already known, and, if the four groups in the set be set down in the usual order, with the characters they are known to carry, the characters carried by the fourth group can be inferred:

Agouti	XYZ
Dilute agouti	
Cinnamon agouti	xYZ
Blue	xYz

[1] See observation 9, p. 25.

Since it is carried by three, Y must be carried by all the groups. The differentiating characters in the set are, therefore, X and x, Z and z, and, since three of the four possible combinations made by these two pairs are already appropriated, the remaining combination, Xz, must belong to dilute agouti, whose three characters are, therefore, XYz.

In Miss Durham's last experiment, cinnamon agouti was mated with silver fawn, and their hybrids' progeny consisted of cinnamon agouti, dilute cinnamon agouti, chocolate, and silver fawn, in the ratio 9 : 3 : 3 : 1. The characters carried by three of these groups are already known, and, if the four groups in the set be set down in the usual order, with the characters they are known to carry against these three groups, the characters carried by the fourth group can be inferred:

Cinnamon agouti	XyZ
Dilute cinnamon agouti	
Chocolate	xyZ
Silver fawn	xyz

Since it is carried by three groups, y must be carried by all four. The differentiating characters in the set are, therefore, X and x, Z and z, and, since three of the four possible combinations made by these two pairs are already appropriated, the remaining combination, Xz, must belong to dilute cinnamon agouti, whose three characters are, therefore, Xyz.

Thus the complete set of eight groups formed by all the possible combinations of X and x, Y and y, Z and z is:

Agouti	XYZ	27
Dilute agouti	XYz	9
Cinnamon agouti	XyZ	9
Black	xYZ	9
Dilute cinnamon agouti	Xyz	3
Blue	xYz	3
Chocolate	xyZ	3
Silver fawn	xyz	1

Still another example of the difficulty of identifying individual factors and their effects is to be found in the experiments on the inheritance of rabbit colours by Major C. C. Hurst and Professor Castle of Harvard. Both experimenters, the one in England, the other in America, were experimenting at the same time, the one on albinism, the other on colour patterns, but the data concerning these may be neglected and those concerning the colours themselves considered.

A black rabbit is sometimes found among wild grey rabbits, more especially in places where the wild race has been mixed with the tame; and young black rabbits have been found in wild litters which could have been the progeny of grey parents only. Obviously grey is dominant to black. Major Hurst bred both grey and black rabbits which bred true. When they were mated, their hybrids were all grey, while the hybrids' progeny were greys and blacks in the proportion 3 : 1 (actually 38 and 10).[1] Thus it is confirmed that grey is a simple dominant to black, and the one-pair set may be written down in the usual way:

G		b
3	:	1

Professor Castle's experiments show this solution to be far too simple, for he found four other colours intermateable with each other and with grey and black: a result suggesting three pairs of factors operating and two more colours remaining to be found. Among the six colours already known, he recorded the following relationships:

1. Grey is dominant to blue-grey, black, and yellow.
2. Blue-grey is dominant to blue.
3. Black is dominant to blue and tortoiseshell,

[1] *Journal of the Linnean Society*, vol. xxix., 1904.

4. Yellow is dominant to tortoiseshell.
5. Grey is got by crossing black with either blue-grey or yellow.

By being dominant to three other groups, grey must carry three dominant characters, and the three groups must each carry two of grey's dominant characters and the recessive of the third. The four groups are obviously the four largest groups in a set of eight, but, since the characters combined in each group cannot be separately identified, the groups must be written down with "unknown" symbols as follows:

Grey	XYZ
Blue-grey	XYz
Black	XyZ
Yellow	xYZ

By being recessive to both blue-grey and black, blue must carry only one dominant, and that dominant must be the one common to both blue-grey and black, namely, X. If it carried Y, its three characters would be xYz, and it would differ from black in three pairs of characters instead of in one. If it carried Z, its three characters would be xyZ, and it would differ from blue-grey in three pairs of characters. It must, therefore, carry the characters Xyz. Similarly, by being recessive to both black and yellow, tortoiseshell must carry the characters xyZ.

The characters carried by the six groups already found and the two not found, so far, with the relative numbers which each group should contain, are:

Grey	XYZ	27
Blue-grey	XYz	9
Black	XyZ	9
Yellow	xYZ	9
Blue	Xyz	3
	xYz	3
Tortoiseshell	xyZ	3

In his paper, "Studies of Inheritance in Rabbits," published in 1909 by the Carnegie Institute of Washington, Professor Castle reports the finding of the two remaining colours, which were described as cream and dilute tortoise.

Cream seems to have been produced for some time without being noticed, and to have been counted among the yellows, for, in reference to the large number of yellows resulting from certain hybrid matings, it is remarked that "the yellow category is probably too large because of a failure to discriminate between yellow and cream, a difference which at first we failed to record." Since their parentage is not stated, the position of these yellows in the set of eight cannot be fixed with certainty, but, since the factor Z seems to intensify blue-grey to grey and blue to black, or, it may be said, z dilutes grey to blue-grey and black to blue, it seems probable that cream is a diluted yellow, carrying the characters xYz, and therefore the sixth colour in the set. Blue and yellow had been mated and their hybrids bred from, and if it be allowed that some of the yellows in the hybrids' progeny were really creams, the kinds produced and their proportions, though the numbers are small, give cream the sixth place in the set and pale tortoise the eighth. The kinds and numbers were:

	Numbers.	*Proportion.*
Grey	20	27
Blue-grey	7	9
Black	8	9
Yellow	12 (?)	9
Blue	4	3
Cream	(?)	3
Tortoiseshell	1	3
Pale tortoiseshell	1	1

In a subsequent experiment, cream and black were mated, and their hybrids' progeny consisted of all the eight colours, in numbers approximating closely to the proper proportions, namely, grey 24, blue-grey 8, black 8, yellow 16, blue 2, cream 3, tortoiseshell 2, and pale tortoiseshell, 2. And, since black carries the characters XyZ, and there is only one other combination, xYz, with which it can be mated and have hybrids whose progeny consist of all the eight groups, that other combination of characters must be carried by cream. The other remaining combination, xyz, must be carried by pale tortoiseshell.

Thus the complete set of eight colours consists of:

Grey	XYZ	27
Blue-grey	XYz	9
Black	XyZ	9
Yellow	xYZ	9
Blue	Xyz	3
Cream	xYz	3
Tortoiseshell	xyZ	3
Pale tortoiseshell	xyz	1

VI

SUPPRESSED EFFECTS

It was seen, in the previous chapter, that two pairs of factors combine to produce the four following kinds of fowls' combs:

Walnut	XY
Rose	Xy
Pea	xY
Single	xy

But Professors Bateson and Punnett found other kinds of combs, and, therefore, other factors.[1] One comb, brought from Cairo, was an ordinary single comb, excepting that it was split in two. This comb was mated with the ordinary single comb, over which it "proved to be a distinct dominant." That is to say, their hybrids were split single combs. Both parents had single combs, and, therefore, carried the characters xy; but the Cairo comb carried a factor for splitting which was dominant to another factor for non-splitting in the ordinary single comb. If we call this new pair of characters S and s, then the Cairo comb carried the characters xyS, the ordinary single comb xys; and, since the other combs in the original two-pair set must also have carried s, the characters carried by the five combs so far considered are:[2]

[1] See the reports to the Evolution Committee and Bateson and Punnett's volumes on Mendelism.

[2] See observation 9.

Walnut	XYs
Rose	Xys
Pea	xYs
Single	xys
The Cairo comb	xyS

and the eight combinations made by the three pairs of factors, X and x, Y and y, and S and s are:

Walnut comb	split	XYS
Walnut comb		XYs
Rose comb	split	XyS
Rose comb		Xys
Pea comb	split	xYS
Pea comb		xYs
Single comb	split	xyS
Single comb		xys

Another kind of comb found was that carried by a Dutch breed of fowl called the Breda. This comb was really no more than a kind of rudimentary comb, but it revealed another pair of characters in operation. It is described thus: "In the cocks there are two minute papillæ"—*i.e.*, pimples—"standing one on each side of the middle line, which are rudiments of a comb structure. As experience shows, the hens have the duplicity of which these papillæ are the evidence, but in examination of the heads of hens practically no comb tissue can be seen or felt."

This Breda comb was mated with both single and rose combs. When mated with single comb, the hybrids had "a large double comb formed as two divaricating singles, not unlike that of the Egyptian." Thus the Breda comb carries the dominant factor for splitting, just as the Cairo comb does. It also carries x and y, for, had it carried X, or Y, or XY, its hybrids, with single comb, would have been split rose, or split pea, or split walnut combs. But it carries still another factor which is recessive to a dominant factor in the single comb which makes their hybrids real combs, not *rudiments*. If we symbolise this pair of factors by r and R, then the factors and characters now known to be carried by the Breda comb and the ordinary single comb are:

Breda	xySr
Single	xysR

And the other combs—walnut, rose, and pea—must also carry R.

This finding was confirmed when the Breda was mated with rose comb. If the Breda comb carry the characters xySr and the rose comb XysR, then they differ in three pairs of characters—y is common to both—their hybrids should be real rose combs, but split, while their hybrids' progeny should consist of the eight kinds formed by the possible combinations of the three pairs of factors X and x, S and s, and R and r, with the factor y common to all kinds. The hybrids were actually split rose combs, but unfortunately, in their progeny, only six different kinds were identified. The following table gives the eight groups which should have been found and the six actually found:

	Groups Expected.		*Groups Found.*
XySR	Rose comb	Split	Duplex rose
XySr	Rose rudiment	Split	Duplex Breda
XysR	Rose comb		Rose
xySR	Single comb	Split	Duplex single
Xysr	Rose rudiment		Simplex Breda
xySr	Single rudiment	Split	Duplex Breda
xysR	Single comb		Single
xysr	Single rudiment		Simplex Breda

The split rudimentary combs were counted as one group only: rose combs and single combs unseparated; and the unsplit rudimentary groups were also counted as one group only: roses and singles again unseparated.

As there are, at least, four pairs of characters operating in fowl combs, the sixteen combinations they can form may now be set down, with the nature of the comb formed by each combination and the common names given to such as have been named:

Combination of Characters.	*Nature of Comb.*		*Common Name.*	*Proportion.*
XYRS	Walnut comb	Split		81
XYRs	Walnut comb	Unsplit	Walnut	27
XYrS	Walnut rudiment	Split		27
XyRS	Rose comb	Split		27
xYRS	Pea comb	Split		27
XYrs	Walnut rudiment	Unsplit		9
XyRs	Rose comb	Unsplit	Rose	9
XyrS	Rose rudiment	Split		9
xYRs	Pea comb	Unsplit	Pea	9
xYrS	Pea rudiment	Split		9
xyRS	Single comb	Split	Cairo	9
Xyrs	Rose rudiment	Unsplit		3
xYrs	Pea rudiment	Unsplit		3
xyRs	Single comb	Unsplit	Single	3
xyrS	Single rudiment	Split	Breda	3
xyrs	Single rudiment	Unsplit		1

It may be that the factor which made the fowls' combs mere rudiments did not suppress the effects of other factors completely. But a factor which completely suppressed the effects of other factors was found in Major C. C. Hurst's experiments with rabbits, already referred to.

Pure-breeding Belgian rabbits, whose colour is given as "yellow-grey," were mated with albino rabbits, and 70 hybrids were produced. All the hybrids, with one exception, were ordinary wild greys. The exception was also a grey, but of another shade. It "had, when young, more yellow on the chest and flanks than the others; but after the second moult, it became almost wild grey like the rest." Thus 69, at least, of these 70 hybrids were like neither parent, a phenomenon of which we have already had two examples. In the first, the hybrids—the Blue Andalusians and the Roan Shorthorns—were intermediates between the two parent kinds; in the second they—the walnut combs—were a combination of a character carried by one parent with that carried by the other. But this example seems parallel to neither, for it is unlikely that the Belgian yellow-grey colour can be darkened either by being mixed with or combined with a colour which contains no pigment at all.

Yet the hybrids indicate more than one pair of factors. Since it is carried by the hybrids, the wild grey colour must either itself be a colour dominant to the Belgian grey colour, or, as is most unlikely, Belgian grey intensified by a factor or factors which are dominant to corresponding recessives in Belgian grey. The result is the same either way. But where does this comprehensive wild grey factor come from? It could not have been carried by the Belgian greys, for then they would have been wild greys. It must, therefore, have been carried by the albinos. The albinos must have carried a factor whose effect was suppressed. So soon, however, as it is transmitted to the hybrids, this wild grey factor has effect, from which it must be inferred that the Belgian greys carried a dominant factor which was handed on to their hybrids, which caused or allowed pigment to be produced, while the albinos carried its recessive, a factor which did not cause, perhaps suppressed, the production of pigment.

If wild grey be represented by W, Belgian grey by b, colour by C, and colourlessness by c, then the factors carried by the two parent kinds should have been:

By the Belgian Greys.	*By the Albinos.*
b	W
C	c

Then the factors carried by the hybrids should have been $\frac{bW}{Cc}$, and the hybrids' progeny should have consisted of the four following kinds, carrying the factors set down below:

Wild Grey Coloured.		*Wild Grey Albino.*		*Belgian Grey Coloured.*		*Belgian Grey Albino.*
W		W		b		b
C		c		C		c
9	:	3	:	3	:	1

That is, 9 wild greys : 3 Belgian greys : 4 albinos.

But the hybrids' progeny were not as expected. They differed from expectation in three ways:

1. There were no Belgian greys among them. "A few individuals appeared to have rather more yellow and less black than the wild grey; but, curiously enough, not one was a true yellow-grey like the Belgian grand-parent."
2. Some litters consisted of greys and albinos; but
3. Others contained blacks also.

The first of these differences may have been, and probably was, due to the Belgian grey factor being accompanied by so many dominant shade factors that too few hybrids' progeny were bred to give the Belgian grey colour a fair chance of appearing again.

The second and third differences show that the hybrids were not all alike, and therefore, since their Belgian grey parents were true-breeding, that their albino parents were not alike. Some may have carried the grey factor only, while others must have carried the black either alone or along with its dominant grey.[1] Then the factors carried by the different kinds of hybrids may have been (putting G for grey, b for black, C for colour, and c for colourlessness):

(*a*) When the albino parent carried grey only $\begin{smallmatrix}GG\\Cc\end{smallmatrix}$

(*b*) When the albino parent carried grey and black $\begin{smallmatrix}Gb\\Cc\end{smallmatrix}$ and $\begin{smallmatrix}GG\\Cc\end{smallmatrix}$

(*c*) When the albino parent carried black only $\begin{smallmatrix}Gb\\Cc\end{smallmatrix}$

Thus there should have been two different kinds of hybrids, and, three different matings being possible, progeny of different kinds and proportions as follows:

$\begin{smallmatrix}GG\\Cc\end{smallmatrix}$ x $\begin{smallmatrix}GG\\Cc\end{smallmatrix}$ should have produced	$\begin{smallmatrix}G\\C\end{smallmatrix}$	$\begin{smallmatrix}G\\c\end{smallmatrix}$
	Greys	albinos
	3 :	1
$\begin{smallmatrix}GG\\Cc\end{smallmatrix}$ x $\begin{smallmatrix}Gb\\Cc\end{smallmatrix}$ should have produced	$\begin{smallmatrix}G\\C\end{smallmatrix}$	$\begin{smallmatrix}G\\c\end{smallmatrix}$
	Greys	albinos
	3 :	1

$\begin{smallmatrix}Gb\\Cc\end{smallmatrix}$ x $\begin{smallmatrix}Gb\\Cc\end{smallmatrix}$ should have produced	$\begin{smallmatrix}G\\C\end{smallmatrix}$	$\begin{smallmatrix}G\\c\end{smallmatrix}$	$\begin{smallmatrix}b\\C\end{smallmatrix}$	$\begin{smallmatrix}b\\c\end{smallmatrix}$
	Greys	albinos carrying Grey	blacks	albinos carrying black
	9 :	3 :	3 :	1
		Greys :	blacks :	albinos
i.e.		9 :	3 :	4

There were actually produced at four matings	Greys 22		albinos 10
i.e.	3 :		1
	Greys	blacks	albinos
At seventeen other matings ..	85	25	30
i.e.	9 :	3 :	4

[1] Professor Castle's experiments showed grey to be dominant to black.

Further experiments were made to show that the albinos carried factors for colours, but carried different combinations of factors. No albino was found carrying the grey factor only, but several were found carrying both grey and black factors and others carrying the black factor only.

The following table shows the kinds of progeny the two different kinds of albinos should have produced with coloured rabbits of different kinds, and the kinds of progeny they actually produced:

	Albinos carrying Grey and Black Factors. Gb cc						*Albinos carrying Black Factors Only.* bb cc					
	Should have Produced.			*Actually Produced.*			*Should have Produced.*			*Actually Produced.*		
	Grey.	Black.	Alb.	Grey.	Black.	Alb.	Grey.	Black.	Alb.	Grey.	Black.	Alb.
With grey pure GG CC	all	—	—	6	—	—	all	—	—	7	—	—
With black pure bb CC	1 :	1	—	20	20	—						
With grey hybrid Gb CC							1 :	1	—	2	2	—
With grey hybrid Gb Cc							1 :	1 :	2	1	3	2
With black hybrid for colour bb Cc	1 :	1 :	2	2	—	1	—	1 :	1	—	6	12

In some of these experiments, the numbers are too small to have the different kinds in the proper proportions; but their total result is sufficient, because no kind was produced which should not have been produced.

A simpler example of suppression occurred among Professors Bateson and Punnett's experiments with sweet peas, the details of which are to be found in the Report to the Evolution Committee. Two white flowered plants of different strains were crossed, and their hybrids had coloured flowers. Unless they were intermediates, which is very unlikely, the hybrid flowers, by differing from both parents, suggest two pairs of factors at least, and four groups of progeny, namely:

Coloured Group.		*Colourless Parent No. 1.*		*Colourless Parent No. 2.*		(?)
X		X		x		x
Y		y		Y		y
9	:	3	:	3	:	1

Since the hybrids between two colourless parents are coloured, it is a fair inference either that colour is produced when the two dominants come together on the same plant, or that colour production is prevented by both the colourless parents' recessive factors. In the latter alternative, the fourth group of the hybrids' progeny should also be colourless, and there should be nine plants with coloured flowers to seven with colourless, as follows:

	Coloured Group.		*Colourless Parent No. 1.*		*Colourless Parent No. 2.*		*Colourless. Group.*
	X		X		x		x
	Y		y		Y		y
	9	:	3	:	3	:	1
i.e.	9	:			7		

When counted, the hybrids' progeny consisted of 2132 plants with coloured flowers, and 1593 with colourless.

If these figures be divided by 232·81, the figure which brings their total to 16, they become 9·16 and 6·84, *i.e.*, 9 : 7.

Among the coloured flowers there was suppression, or, at any rate, something which prevented complete separation of kind from kind. Three pairs of factors were found to be operating, namely, a purple factor, say P, dominant to red, say r; a densing factor, say D, dominant to a diluting, say d; and a factor which made the standard portion of the flower darker than the wing, say B, which may be named bicolouring, dominant to another which left the flower unicoloured, say u. With these three pairs of factors operating, there should have been eight different colours among the hybrids' progeny, namely:

1	2	3	4	5	6	7	8
D P B	D P u	D r B	d P B	D r u	d P u	d r B	d r u
Dense purple bi-colour.	Dense purple uni-colour.	Dense red bi-colour.	Dilute purple bi-colour.	Dense red uni-colour.	Dilute purple uni-colour.	Dilute red bi-colour.	Dilute red uni-colour.
Purple invincible.	Deep purple.	Painted Lady.	*Picotée.*	Miss Hunt	*Picotée.*	*Tinged white.*	*Tinged white.*

These four kinds, printed in ordinary type, which could be associated with the groups above their names, were found. The two kinds printed in italics were also found. The first were probably groups 4 and 6 together, the second groups 7 and 8.

Among both animals and plants the word "white" needs very careful watching. Among fowl there are "white" breeds which have small specks of colour, and, so, are not really white. So also there are "wild white" cattle which have small areas about the ears, eyes, nose, and sometimes the legs, coloured black, or red, or brown. The " wild white " cattle are recorded to have thrown black or red calves in the past, and, ten or twelve years ago, two which were confined in the London Zoological Gardens threw black calves. These cattle are really coloured cattle carrying a factor for blackness or redness, as the case may be, along with other factors which restrict the production of colour to the areas mentioned above. The colour factors and the restriction factors are independent of each other, and the restriction factors are generally recessives to others connected with the more general distribution of colour.

VII

SIMILAR EFFECTS

SINCE about 1890, an enormous amount of work in the production of new and better farm crops has been done at Svalöf, in Sweden. Since the discovery of Mendel's papers, in 1900, this work has increased greatly both in quantity and precision, and no section has been more successful than that concerned with raising improved grain crops which, till a few years ago, was under the charge of Professor Nilsson-Ehle, now of the University of Lund. That part of his work which we are now to consider is described in two papers "Kreutzunguntersuchungen an Hafer und Weitzen" (Crossing Experiments with Oats and Wheats), published by the University of Lund in 1909 and 1911.

Among oats there are five or six different colours of grain, namely, black, brown, tawny, grey, yellow, and white. Some colours are not easily defined, however, and it would be dangerous to say that there is either an absolutely black or an absolutely white grain. What is generally called "black" is a very dark brown, and what is generally called "white" is a more or less faded cream or dull white. Besides, there are shades in every colour, and the lighter shades of a darker may not be readily distinguishable from the darker shades of a lighter colour.

The existence of so many colours indicates a considerable number of colour factors, with, perhaps, as many shade factors in addition. Nor is it unlikely that the same colour may get one name from one observer, another from another.

A number of " black " oats were crossed with " white," and the hybrids were found to be browns of several different shades. This indicated either that there were more than one pair of factors, or that the browns were intermediates between the blacks and the whites. The hybrids' progeny were still more diverse, but the browns and blacks of all shades were counted together as one kind, and it was found that, on the whole, they were to the whites in the ratio 3 : 1. Thus " black " was taken to be dominant to " white."

A white variety, No. 0353, was crossed with two black varieties, Nos. 0401 and 0487, and the hybrids were brown in both cases, but, when the hybrids were bred from, their progeny were blacks and whites in the ratio 3 : 1. The actual figures and ratios were:

Parents.	*Hybrids.*	*Hybrids' Progeny.*		*Ratio.*
0353 x 0401	brown	86 " black "	33 white	2·6 : 1
0353 x 0487	,,	104 ,,	46 ,,	2·3 : 1

The same white variety was crossed with two other " black " varieties, and other factors were revealed. The hybrids' colours are not stated, but their progeny's colours and the numbers in each kind were as follows:

Parents.	*Hybrids' Progeny*		
	Black.	*Grey.*	*White*
0353, white x 0660, black	107	19	5
0353, ,, x 0691, ,,	216	51	25
	323	70	30

The blacks are about three times as many as the greys and whites together, and the greys about three times as many as the whites. Thus, we may have the following two-pair set:

X	X	x	x
Y	y	Y	y
9 :	3 :	3 :	1
12 :		3 :	1
Black		Grey	White

But the same white variety was mated with still another black, and still another pair of factors was suggested. The hybrids' colours are not stated, but four of them were bred from, and their progeny were as follows:

Parents.	Hybrids.	Progeny. Black.	Progeny. Grey and White.	Ratio.
0353, white x 0668, black	a	207	12	17·8 : 1
	b	116	7	16·6 : 1
	c	191	13	14·7 : 1
	d	116	8	14·5 : 1

Since this experiment shows the blacks to be to the greys and whites together as 15 : 1 and the previous experiments showed the blacks to be to the greys as 3 : 1, the ratio for the three together is black : grey : white=60 : 3 : 1, which suggests a three-pair set of eight groups, as follows:

X	X	X	x	X	x	x	x
Y	Y	y	Y	y	Y	y	y
Z	z	Z	Z	z	z	Z	z
27 :	9 :	9 :	9 :	3 :	3 :	3 :	1
60						3 :	1
Black						Grey	White

That is to say, there are six groups of inseparable blacks. And we may take it that the two factors X and Z produce approximately the same effect whether they occur separately or on the same plant together and that the result is still approximately the same even when Y occurs along with them: the factor which has to do with the production of greyness.

Professor Nilsson-Ehle carried his experiments on to another generation, by which the foregoing inference was confirmed; but, since the experiments and arguments with these oat grains are parallel to others with wheat grains, we shall take those with the wheat grains as standing for both.

The first experiments indicated that the red colour in red-grained wheat is dominant to the white colour in white-grained, and that the two colours differ in one pair of characters, thus:

The Parents.		*The Hybrids' Progeny.* Red.	White.	*Ratio.*
0401, red x 0705, white		31	9	3·4 : 1
0203, ,, x 0705, ,,		72	28	2·6 : 1
0235, ,, x 0470, ,,	a	32	6	5·3 : 1
	b	67	13	5·2 : 1
	c	63	15	4·2 : 1

With regard to these results, Professor Nilsson-Ehle remarked: "The first two crossings obviously follow the monohybrid scheme. The red-grained individuals could always be distinguished from the white without difficulty. In the crossings 0235 x 0470, the reds are in all cases more numerous than they should be, but, with such small numbers of individuals, such deviations could be accidental. So far, however, the crossing has not been followed into F 3 (*i.e.*, into the next generation), and a closer explanation of this comparatively strong deviation cannot, as yet, be given."

But the next experiments had a different result. The parents and their hybrids' progeny were as follows:

The Parents.		*The Hybrids' Progeny.* Red.	White.
0315, white x Swedish Sammet wheat, red	a	78	0
	b	30	0
	c	49	0
	d	31	0
	e	86	0
	f	110	0
0704, white x 0501, red		55	1

The first six of this set of experiments, in which 384 reds and no whites were produced, suggest four pairs of characters at least, with four red factors dominant to four whites. If this suggestion be correct, there should be one white grain in every 256, on the average. But if there be four pairs of factors, a white grain has a very small chance of appearing in any one of these experiments. Even if there were only three pairs of factors, and there should be one white grain in every 64, the chances of such a grain appearing are favourable in three of the experiments only, and then they are only 1·2, 1·3, and 1·7 to 1. Thus it is not impossible that there may be only three pairs of characters, as is suggested by the seventh experiment. Professor Nilsson-Ehle took the view that this assumption might be correct, and, in order to test it, sowed all the seeds of the 78 plants grown in experiment a separately. If there were 63 such plants, they should consist of:

37 producing reds only.
8 producing reds and whites in the ratio 63 : 1,
12 producing reds and whites in the ratio 15 : 1, and
6 producing reds and whites in the ratio 3 : 1.

But there being 78,[1] they should consist of:

45 producing reds only,
10 producing reds and whites in the ratio 63 : 1,
15 producing reds and whites in the ratio 15 : 1, and
8 producing reds and whites in the ratio 3 : 1.

[1] Multiply the figures in each group by $\frac{78}{64}$.

When their seeds were counted, there was considerable difficulty in deciding to which kind some of the plants belonged. Plants producing 65 or more red seeds and no whites could be assumed to be producers of red grains only, but, if a plant produced from 60 to 25 red grains and no whites, there was doubt as to whether it was a producer of red seeds only or of red seeds and white in the proportion 63 : 1. Still further, plants producing less than about 25 red grains and no whites might be either 15 : 1 or 63 : 1 plants, or even plants producing red grains only.

In the table on p. 66, the whole 78 plants are grouped according to the seeds they actually produced.

Allowing for the doubt as to whether some of the figures towards the bottom of the first column should remain where they are or be placed in the second, or even in the third column, the result, especially in the last two columns, is so close to what was expected, if there were three factors producing red dominant to three producing white, that, we may take it, there were actually three such pairs.

Professor Nilsson-Ehle found the differences between different red grains on the one hand and different whites on the other very slight. Thus, so far as colour production is concerned, it makes little difference whether one, two, or all three red factors are operating. "It can be asserted that the differences in the externally visible effects of the various units for the red grain colour are quite inconsiderable, and that, in any case, nothing can be said as to a qualitative distinction; less even than in the black coat-colour of the oat. . . . The units produce only a slightly different shade of red."

Producing Reds Only.			*Producing Reds and Whites.* 63 : 1			*Producing Reds and Whites.* 15 : 1			*Producing Reds and Whites.* 3 : 1		
No.	*Red.*	*White.*	*No.*	*Red.*	*White.*	*No.*	*Red.*	*White.*	*No.*	*Red.*	*White.*
35	167	0	70	125	2	17	52	2	53	9	2
64	152	0	40	61	1	50	24	1	16	29	7
69	108	0	12	51	1	68	47	2	18	33	9
6	95	0	74	45	1	1	42	2	43	68	21
66	88	0	45	42	1	72	40	2	37	38	12
3	85	0				21	37	2	41	55	18
4	82	0				71	59	3	55	33	11
65	74	0				78	14	1	7	42	17
39	73	0				15	41	3			
75	72	0				38	81	6			
14	69	0				19	52	4			
48	69	0				59	25	2			
8	65	0				13	60	6			
47	61	0				73	86	9			
22	58	0				76	67	8			
44	58	0									
67	58	0									
11	57	0									
49	56	0									
20	49	0									
58	47	0									
77	42	0									
9	37	0									
51	38	0									
54	37	0									
46	36	0									
56	36	0									
28	34	0									
29	34	0									
57	32	0									
36	30	0									
34	29	0									
23	26	0									
27	25	0									
4	24	0									
33	23	0									
52	23	0									
10	21	0									
26	18	0									
60	18	0									
2	15	0									
32	15	0									
5	13	0									
24	13	0									
25	13	0									
61	13	0									
62	12	0									
63	7	0									
30	6	0									
31	4	0									

i.e. 50 : 5 : 15 : 8

55 : 15 : 8

Nos. expected: 45 : 10 : 15 : 8

55 : 15 : 8

VIII

POLYGAMY

AMONG horses there are five intermateable colours—grey, dun, bay, black, and chestnut—and a series of shade factors which have little or no identifiable effect upon grey and black, but vary chestnut from bright gold, near one extreme, to dark liver, near the other, bay from light bay to dark brown, and dun from cream to dark or bluish dun. As yet, little is known about the shade factors, and in what follows they are neglected. In addition to these, there is a pair of factors whose effects are readily recognisable in every colour but grey. The dominant mixes the coat with grey hairs—makes the animal a roan—while the recessive leaves it unmixed. There are, therefore, chestnut, black, bay, dun, and grey roans, but the last cannot be identified unless the animal be very young. The roaning factor affects the body only and leaves the face and the lower limbs the normal colour. A grey horse is not born grey, but usually black or very dark brown. The greying begins about the head and face and at the root of the tail, with the casting of the first coat. Thus a foal with black legs and face, but its body a mixture of black and white hairs, may be either a black roan or a grey roan. If its face remains black, it is a black roan; if the face turns grey, it is a grey roan. Two roans have not been mated very often, consequently horses pure-breeding for roan have not been easily found. So far only one, and that in America, has been identified, but, since hybrid roans produce equal numbers of roans and normals, when mated with normals, and two normals do not produce a roan, the dominance of the roaning factor is clear.

According to the Mendelian scheme, five colours—five groups—is an unusual number, and, unless three others are found, as the remaining mice and rabbit colours were found by Miss Durham and Professor Castle, it must be assumed that the factors which produce horse colours operate in an unusual manner. So far, though these five colours have been intermated frequently, the stud book records which have been examined and information collected from other sources reveal no other colour.

The earliest important evidence as to the inheritance of horse colours was that collected from the records of German state studs by Drs. M. Wilckens and H. Crampe, and published as far back as 1887 and 1888 in volumes xvii. and xviii. of "*Landwirtschaftliche Jahrbücher.*" Dr. Crampe makes two very significant observations, namely:

1. That chestnuts with chestnuts throw chestnut foals, including chestnut roans and chestnut greys.

2. That blacks with blacks throw black and chestnut foals, and roans and greys of these colours.

Since chestnut roans and black roans are merely chestnuts and blacks carrying the additional effect of another factor and greys are very liable to misdescription, we can infer that chestnut is recessive to all other colours and that black, by throwing blacks and chestnuts only, is a simple dominant to chestnut and recessive to the others.

The first of these inferences is confirmed by the Suffolk Punch breeders, while the second is confirmed by data collected by Dr. Walther in the records of the

Trakehnen, Beberbeck, and Haltburn studs, published in his "Beiträge zur Kentniss der Vererbung der Pferdefarben" in 1912. Excluding three grey entries as erroneous, he found that black with black threw 852 black foals and 74 chestnuts.

The first inference was also confirmed by Major Hurst's data, collected from the Thoroughbred stud book, that is, Weatherby's "General Stud Book," and published in the "Proceedings", of the Royal Society in 1906. But Major Hurst made another inference of no less importance, namely, that bay is also a simple dominant to chestnut. His figures are :

	Bay Foals.	*Chestnut Foals.*
With chestnut mares, 101 chestnut sires get	9	1095
With chestnut mares, 6 pure bay sires get	379	0
With chestnut mares, 12 hybrid bay sires get	355	347

Had bay been other than a simple dominant to chestnut—*i.e.*, differing from it in more than one pair of characters—equal numbers of bays and chestnuts would not have been thrown.

Still another inference is suggested, namely, that grey is dominant to bay. Otherwise these bay sires, in a breed containing greys, would surely have thrown some grey foals.

Thus bay and black are both dominant to chestnut. How do they stand to each other? So far, the behaviour of these three colours is parallel with that of the fowls' combs, at the stage when both rose and pea were found dominant to single comb. But the parallel goes no farther, for, when bay and black are mated, no new colour is produced: only bays and blacks, and chestnut, their common recessive. Two sets of figures are available: one from Dr. Walther's volume, the other from the stud book of the English Shire Horse Society:

	Bays.	Blacks.	Chestnuts.
With black German mares, 68 bay sires got	281	124	20
With black Shire mares, 28 bay sires got	409	225	35

No clear inference can be drawn from the relative numbers of each colour, because it is impossible to say how many of the bay sires were hybrid and how many pure. Since some of the bay sires must have been pure, the preponderance of bay foals over both blacks and chestnuts suggests that bay is dominant to black as well as to chestnut. But this would not explain the non-appearance of a fourth colour. How, then, is the phenomenon to be explained? It might be suggested that there are two pairs of characters and two inseparable bay groups, according to the scheme:

X	X	x	x
Y	y	Y	y
Bay		Black	Chestnut

But this would mean that bay differs from chestnut in two pairs of characters, a conclusion which is opposed to that suggested by Major Hurst's figures. Obviously, there are not two pairs of characters, and, since there are three colours, there must be three factors, each of which mates with the other two severally and indifferently. If this be so, then, since there is no fourth colour, either black or bay must be dominant the one to the other and the two must differ from each other in one pair of characters only. In the Shire stud book, 14 sires were found which, by their progeny with bay mares, were pure bays; and these sires, with black mares, got bay foals only. Dr. Walther also found 11 German sires which, with black mares, got bay foals. Thus bay is dominant to black. The actual figures, with presumably erroneous entries enclosed within brackets, are:

	Bays.	*Blacks.*	*Chestnuts.*
With bay mares, 14 bay sires got	618	(2)	(2)
With black mares, the same sires got	163	(6)	—
With black mares, 11 German sires got	200	—	(9)

But in how many factors do bay and black differ? Sixteen bay sires got both bays and blacks, when mated with bay mares, and thus showed that they carried the black factor as well as the bay. When mated with black mares, they got equal numbers of bay and black foals. Dr. Walther found 10 similar German bay sires. Thus bay differs from black in one pair of characters. The figures, with presumably erroneous entries enclosed within brackets, are:

	Blacks.	*Bays.*	*Chestnuts.*
With bay mares, 18 bay sires got	366	57	(3)
With black mares, the same sires got	51	41	(1)
With bay mares, 10 bay German sires got	141	28	(1)
With black mares, the same sires got	105	98	—

We have, therefore, a series of three colours—bay, black, and chestnut—in which bay is dominant to black and chestnut and black to chestnut, and each is the result of one factor only which mates with either of the others, but only with one other at one time. There should, therefore, be bays pure, bays carrying black and bays carrying chestnut, blacks pure and blacks carrying chestnut, and chestnuts pure, as indicated in the following table, in which By stands for the bay factor, Bl for the black, Ch for the chestnut; and the pure colours are indicated by a double dose of the factor they carry:

	Bay.	*Black.*	*Chestnut.*
Pure	By By	Bl Bl	Ch Ch
Hybrid for chestnut	By Ch	Bl Ch	
Hybrid for black	By Bl		

If this hypothesis be sound, then, in a breed containing the three colours mated at random, or, at any rate, without undue preference for any colour, the progeny of the bay sires should fall into three and the progeny of the black sires into two different assemblages of colours, as indicated below:

			With Bay Dams.			*With Black Dams.*			*With Chestnut Dams.*		
			Bay.	*Blk.*	*Cht.*	*Bay.*	*Blk.*	*Cht.*	*Bay.*	*Blk.*	*Cht.*
Pure bay sires	(By / By)	should leave	x	—	—	x	—	—	x	—	—
Bays carrying black	(By / Bl)	,,	x	x	—	x	x	—	x	x	—
Bays carrying chestnut	(By / Ch)	,,	x	x	x	x	x	x	x	—	x
Blacks pure	(Bl / Bl)	,,	x	x	—	—	x	—	—	x	—
Blacks carrying chestnut	(Bl / Ch)	,,	x	x	x	—	x	x	—	x	x

The following table gives the colours of the progeny of 68 bays and 16 black Shire sires, when mated with mares of the three different colours. Obviously erroneous entries are again enclosed within brackets:

	With Bay Dams.			With Black Dams.			With Chestnut Dams.		
	Bay.	Blk.	Cht.	Bay.	Blk.	Cht.	Bay.	Blk.	Cht.
Fourteen bay sires got	616	(2)	(2)	163	(6)	—	68	—	(4)
Eighteen bay sires got	366	57	(3)	51	41	(1)	35	9	(1)
Thirty-six bay sires got	1296	92	134	167	83	19	103	(16)	88
Four black sires got	13	12	—	(1)	19	—	(3)	11	—
Twelve black sires got	266	75	37	(3)	53	8	(1)	7	17

Thus, the progeny of bay and black sires fall into the expected assemblages, and our hypothesis that the colours bay, black, and chestnut are each due to single factors which mate with each other indifferently, but only one at a time, is proved. Among the figures there is only one serious discrepancy: that for the foals of 36 bay sires with chestnut mares. Among horse-owners, perhaps the most frequent misdescription is calling a horse black which is not black, but very dark brown. Five of the sixteen foals which were presumably described erroneously were the progeny of a horse so very dark brown that he was usually called a black. Less frequently a light bay is misdescribed as a chestnut or a chestnut as a bay. The readiest distinguishing marks are that bays and browns have black "points" and manes, and, usually, tan muzzles, while blacks are black all over and chestnuts chestnut all over, even to the mane.

But what of the remaining two colours, grey and dun? Are they further members of the same series with bay, black, and chestnut? It would be very surprising if they were not, but materials to prove that they are have been few and hard to find.

Because of their paucity in modern British breeds, both greys and duns are very short in data, and reliance has to be placed on early Thoroughbred records supplemented by information collected from smaller modern breeds and among unregistered stock. Besides, grey data must be handled with unusual care. Because they are not born grey, grey horses are often registered as of some other colour, and the original misdescription is not often corrected. The foal which is eventually to be a grey may be a dull black or some very dark shade of what looks like chestnut or brown. The first grey hairs usually appear with the casting of the first coat, most conspicuously about the head and the root of the tail, and the greying increases with every new coat till, in seven or eight years, the body is quite grey and the legs obviously becoming so. Eventually, all is grey, and, if the horse live long enough, white.

While the data were being collected, it soon became obvious that at least one of the parents of every grey horse is a grey. Some greys may have two grey parents, but all have one. From this it was inferred that grey is dominant to all the other colours, but complete proof was not found for some time. The difficulty was to find a grey which bred true and was, therefore, pure. By allowing for the error of misdescription, two English Thoroughbreds, the Coombe Arabian, with 19 grey foals out of 20, and Rib, with 11 out of 12, might have been relied upon, but two horses only, neither with a very large number of foals, and both dead a century and a half, could not be pressed too far. Eventually, however, evidence was found which set the dominance of grey to other colours beyond dispute. Mr. Robert Bunsow found that Celle Amurath, a grey Arabian belonging to the Prussian Government, had got 600 foals from mares of all colours, and every foal was grey. Dr. Walther also found that a grey sire called Zigeuner had got 13 foals from grey mares and 46 from mares of other colours, and all were grey but one, which died young.

Dun's position was even more difficult to decide, for the data were old and scanty. Dun was a Thoroughbred colour till about the end of the eighteenth century, and it was found that every dun in the stud book whose parents' colours could be determined had one parent which was dun. It was also found to be similar with most of the duns registered in the more recent pony stud books. Thus dun seemed to be dominant to all other colours, not excepting even grey. But, when the records of their progeny were examined, it was found that, though they leave all colours, they leave no grey unless the other parent be a grey. Thus dun is recessive to grey and dominant to the other colours. The best proof of this was given by the progeny of three dun sires which were sent in succession by the Irish Government for service on Clare Island, off the coast of Mayo. The mares on the island were of the usual colours: bays, browns, blacks, and chestnuts: and there were no other sires on the island. The progeny of the first two sires, Oscar, used from 1901 to 1903, and Norseman, from 1904 to 1906, were all duns. The third dun sire was sent to the island in 1908, and, while more than half his progeny were duns, the remainder were of the usual colours, with one grey exception, which was out of a grey mare.

Thus we have a series of five colours—grey, dun, bay, black, and chestnut—in which those coming foremost are dominant to those coming after them, and those coming hindmost recessive to those coming before them. But the question still remains: Are grey and dun, like bay, black, and chestnut, the result of single factors which are polygamous? If so, then there should be greys and duns carrying the following factors:

Greys.

Gr	Gr	Gr	Gr	Gr
Gr	Dn	By	Bl	Ch

Duns.

Dn	Dn	Dn	Dn
Dn	By	Bl	Ch

And each of these kinds should produce different assemblages of colours when mated with different colours. Consider the greys first.

1. Pure greys, $\frac{\text{Gr}}{\text{Gr}}$, should leave grey foals only.

2. Hybrid greys with hybrid greys should leave grey foals and foals of other colours, but the greys should be to the other colours as 3 : 1. For the factors offered are:

	By the Sires.	*By the Dams.*	
	....................Gr	Gr....................	
	and	and	
	....................By	By....................	
or	....................Dn	Dn....................	or
or	....................Bl	Bl....................	or
or	....................Ch	Ch....................	or

And the chances are equal that Gr in the sire will unite with either Gr or with the recessive factor, whichever is carried, in the dam, or that the recessive factor, whichever is carried, in the sire will unite with Gr or with the recessive factor in the dam. Then, if there are sufficient matings, the chances are that the following combinations, putting re for any recessive factor, will be formed:

Gr	Gr	re	re
re	re	Gr	re
Grey	Grey	Grey	Recessive
1 :	1 :	1 :	1
	Grey		Recessive
i.e.	3 :		1

3. Hybrid greys with other colours should leave equal numbers of grey foals and foals of other colours, for the chances are even that either the grey or the recessive factor, whichever it is, in one grey parent will unite with a factor recessive to grey in the other parent.

4. None of the progeny of hybrid greys, whether one or both parents are grey, should carry a colour lower in the scale, reckoning grey at the top and chestnut at the bottom, than that produced by the recessive which is the higher of those carried by either parent. For example, a hybrid grey sire, or dam, whose recessive factor is bay, should have no foals lower in the scale than bay; while a grey whose second factor is chestnut might have foals of any colour from grey down to chestnut, but, if mated with other parents whose lowest recessive is bay, should have no foals lower in the scale than bay.

The following are the different assemblages of colours produced by grey matings. They are arranged in the same order as the predicted matings above to which they correspond:

1. Four grey sires have been found producing greys only, namely:

Sires.	*Progeny.*	
	Grey.	*Other Colours.*
The Coombe Arabian	19	(1)
Rib	11	(1)
Celle Amurath	600	—
Zigeuner	58	(1)

2. In 69 grey x grey matings, all probably hybrid x hybrid, among early Thoroughbreds, there were produced:

Greys.	*Other Colours.*
53	16

3. In 413 matings of grey with some other colour there were produced:

	Greys.	*Other Colours.*
Among early Thoroughbreds	140	144
Among Shire horses	64	81

4. The following table gives the progeny of 18 hybrid grey sires when mated with mares of other different colours. It will be noticed that the first five sires had no foals lower in the scale than bay, the sixth none lower than black, while the rest had foals carrying chestnut, the lowest colour in the scale. It will also be noticed that there are no dun foals. No grey x dun matings were found. The sires were all Thoroughbreds excepting those against whose names the letter (S) is placed, which were Shires. The date against each sire's name is approximately that of his birth.

Sires.	*Progeny.*			
	Grey.	*Bay.*	*Black.*	*Chestnut.*
Gimcrack, 1760	12	9	—	(1)
Bell's Arabian, 1760	9	5	—	—
True Britain, 1858 (S)	24	35	—	—
Lincolnshire Lad, 1872 (S)	64	79	(2)	(1)
Buchanan, 1877	26	29	—	(1)
The Colonel (S)	6	5	3	—
Crab, 1722	23	9	3	3
Starling, 1727	19	14	4	2
Blank, 1740	14	13	—	4
Panton's Arabian, 1750	15	4	—	4
Mambrino, 1768	19	8	—	4
Bordeaux, 1774	29	12	—	2
Delpini, 1781	46	23	—	10
Strathconan, 1863	92	71	—	37
Sir John Falstaff, 1873 (S)	11	9	4	3
Pepper and Salt, 1882	38	17	—	20
Grey Friars, 1883	48	37	1	8
Grey Leg, 1891	54	22	—	34

The hypothesis might be tested still further by the progeny of the last five sires, who, because they were born in the nineteenth century, may have the more accurate records. The sires themselves carried, as their second factor, chestnut. With chestnut mares, therefore, they should have had grey and chestnut foals only in equal proportions. Their actual progeny with such mares were:

	Grey.	*Bay.*	*Chestnut.*
Strathconan	24	(3)	16
Sir John Falstaff	2	—	2
Pepper and Salt	17	—	7
Grey Friars	15	(3)	4
Grey Leg	13	(1)	15

The data concerning duns are too few to give a similarly full discussion. One result, however, is sufficient to show that it is parallel with the other colours. When hybrid duns were mated with colours lower in the series, equal numbers of duns, on the one hand, and of the other colours, on the other, were produced. The numbers are: duns 55, bays 43, blacks 9, and chestnuts 3. A dun Thoroughbred, Brilliant, foaled in 1750, got 5 duns, 1 bay, 1 black, and 1 chestnut with bay mares, and 1 dun and 1 chestnut with chestnut mares.

It is just possible that this series of colours does not end with the chestnut horse, but continues down to those of the donkey and the zebra, for both donkey and zebra colours are recessive to the horse colours. Little more can be said about these other colours, however, because the hybrids do not breed. This can be said, however, that mules—*i.e.*, horse x donkey hybrids—are always one or other of the five horse colours, with every colour's particular idiosyncrasy. Chestnut mules are wholly chestnut, black mules are wholly black, bays (and browns) have black "points," black manes and tan muzzles, dun mules have black points, and grey mules become grey gradually, just like grey horses.

And not the least interesting inference from these results is that Lord Morton's famous quagga hybrid was, in all probability, not a hybrid at all. Excepting for the striping, which is due undoubtedly to other factors, Professor Cossar Ewart's famous zebra hybrids, bred in his experiments at Penicuick, were all one or other of the horse colours. The zebra colour is, therefore, also recessive to the horse colours. In all probability, so also was the quagga colour, and, if that be so, it was impossible for Lord Morton's quagga stallion to have had a bay foal, as the so-called hybrid was, with a chestnut mare.

Just as there are only five colours among British horses, so there are only five true-breeding colours among British cattle; and, as this unusual number of horse colour groups indicated that the colour factors must operate in an unusual manner, so this unusual number of cattle colour groups indicates that the cattle colour factors also operate in an unusual manner. No records have been found of the mating of white with brown or steel dun, but the other colours and their intermediate hybrids are frequently intermated. Yet no new colour is recorded.

The problem may be made clear by considering the results of three intermatings which are well known. Black differs from red in one pair of characters and from white also in one pair, leaving dominance aside. Usually the two-pair sets of which they seem parts would be written down as either:

			—	XY
Black	XY	or	Red	Xy
Red	Xy		White	xY
White	xY		Black	xy
—	xy			

In the former case, red x white should produce a common recessive, at the second cross, and, in the latter, they should produce a common dominant, at the first cross, while red should be dominant to black. But no such products arise, and red is recessive to black. The only alternative is that the three colours—black, red, and white—are each produced by single factors, and that these factors are polygamous. If this be so, then blue roan, the hybrid between black and white, and red roan, the hybrid between red and white, should produce equal numbers of blacks, blue roans, red roans, and whites. Representing the hybrids by their parents' initials:

Blue Roan.	x	*Red Roan.*
......................B		R......................
......................W		W......................

should produce

B	B	W	W
R	W	R	W
Black	Blue roan	Red roan	White
1 :	1 :	1 :	1

In some parts of Ireland, a few blue roan cows and heifers are mated with Shorthorn bulls, and some of the county instructors and overseers in agriculture very kindly collected what information they could gather as to the results of mating blue roans with red roan Shorthorns. The figures they got are not completely satisfactory, but, if it be remembered that the blue roans belonged mostly to small farmers, who generally spoke from memory of animals no longer in their possession and had no less difficulty in distinguishing roans from blacks or reds than Shorthorn breeders have had in distinguishing red roan from red, it will be seen that the possible discrepancies are not too many. The figures were:

Black.	*Red.*	*Blue Roan.*	*Red Roan.*	*White.*
12	(7)	38	26	30

Among Highland cattle there are four colours—black, red, brown, and light dun—and their hybrids. For our purpose, Highland cattle records are not ideal, but there are no others containing information about light duns, browns, and their hybrids. Even so, the information is not plentiful, for the breeders have been partial to certain colours—yellows, and brindles, and reds—and against the others. Consequently, many a black calf, some duns, and nearly every brown is not registered at all. Besides, Highland colours are very liable to misdescription. Many blacks, fewer reds and yellows, are really brindles, and distinguishing adjectives are not always given to the duns. Thus, of the possible matings, we must use only those in which the chances of error are smaller, in order to discover whether the colours they produce are as predicted. In the first of each two lines in the following table are set down the colours which should be produced by different matings, in the second the numbers actually produced, as recorded in vols. xiii., xiv., and xv. of the Herd Book.

	Black.	*Red.*	*Brindle.*	*Yellow.*	*Dun.*	*Light Dun.*
Red x Light dun						
R x L	—	—	—	x	—	—
R L	—	(1)	—	11	—	—
Black x Light dun						
B or B x L	—	—	—	x	x	—
B r L	—	(1)	—	1	3	—
Yellow x Yellow						
R x R	—	x	—	x	—	x
L L	(1)	15	(5)	40	5	8

	Black.	*Red.*	*Brindle.*	*Yellow.*	*Dun.*	*Light Dun.*
Red x Yellow						
R x R	—	x	—	x	—	—
R L	(2)	77	(27)	92	(4)	(1)
Yellow x Light dun						
R x L	—	—	—	x	—	x
L L	—	—	—	4	2	2
Black x Dun						
B or *B* x B	x	—	—	x	x	—
B r L	—	—	—	1	3	—
Black x Yellow						
B or B x R	x	x	—	x	x	—
B r L	18	5	(8)	19	16	—
Yellow x Dun						
R x B	x	—	—	x	x	x
L L	1	—	—	4	2	3

The only serious discrepancies are the brindles, but they, because of the possible misdescriptions of their parents, may be neglected. The duns produced in the crossings yellow x light dun and yellow x dun are probably light duns without the distinguishing adjective. Though brown entries are not now made in the Highland Herd Book, it was found that brown Longhorns and Jerseys produced brindle hybrids with other colours, and that these brindles reproduced browns again. Consequently, we may say, with a considerable degree of probability, that the five colours—black, red, white, brown, and light dun—are produced by single factors which are polygamous.

IX

COUPLING OR LINKING

The outstanding features in sex are the numerical equality and the physical inequality of males and females. With some unusual methods of reproduction, one sex is more numerous than the other, but, ordinarily, the two are numerically equal.

Males and females usually differ from each other in a number of characters, and the differences are such that the sexes of familiar species may be distinguished at a glance. The differences are usually in size, strength, vigour, and shape, but sometimes there are differences in coat markings and patterns, and even in general colour. Thus there are characters coupled or linked; and, since the sexes are generally equal in number and, at the same time, carry different characters, it may be that a theory which will explain one of these phenomena may, at the same time, explain or help to explain the other.

The numerical equality of the sexes itself suggests an inference. When a pure kind is mated with its hybrid, the progeny consist of equal numbers of the pure kind and the hybrid. Is it possible that either the male or the female character is a hybrid? This hypothesis would account for the production of equal numbers of males and females. But which is the hybrid? Let us assume, in the meantime, that the female is the hybrid. If the assumption be wrong, it can be altered.

But is this hypothesis consistent with the phenomenon that certain definite characters accompany one or other sex? If it be so with one set of animals, it may be so with others.

There is a certain breed of fowl, called the Barred Plymouth Rock, on whose feathers the distribution of the black general colour is not continuous but interrupted by cross-bars of a lighter shade. This breed is now over half a century old, and is known to have originated in a cross in which one parent was a barred breed called the Dominique, a native of the West Indies. In the Barred Rock breed, an occasional black chicken—that is, an unbarred chicken—is thrown, though both parents are barred. Thus barring is dominant to non-barring.

There are said to be strains of the breed in which, through persistent elimination of offending parents, no black chickens have been thrown for many years, but in the breed as a whole these unwelcome black chickens still appear; and the extraordinary thing about them is that they are all hens. Non-barring being recessive, these black chickens must be pure for the non-barring and must have received a non-barring factor from each parent. Their parents, therefore, must both be hybrids, carrying factors for both barring and non-barring. Putting B for barring and b for non-barring, they may be represented in characters and factors thus:

Males.	*Females.*
B	B
b	b

But why does no male chicken get a second non-barring factor? It must be that the barred hens cannot hand on their non-barring factor to their sons; that it is tied up with, coupled, or linked with the factor for femaleness, and must always remain with the sex carrying that factor. The hypothesis now is that

Barred Rock fowl usually carry the following factors, putting M for male, F for female, B for barring, and b for non-barring, and enclosing the tied factors within brackets:

Cocks.	*Hens.*
MM BB	M [F] B [b]

but that the Barred Rock fowl which throw barred cock chickens and non-barred, or black, hen chickens carry these:

Cocks.	*Hens.*
MM B b	M [F] B [b]

The male progeny of such parents must take M and B from their dams, but M and either B or b from their sires. The female progeny, on the other hand, must take F and b from their dams, but, like the males, M and either B or b from their sires. The progeny of Barred Rock fowl which throw non-barred hen chickens should consist, therefore, of the four following kinds:

MM BB	MM B b	M [F] B [b]	M [F] b [b]
Barred cocks		Barred hens	Non-barred hens
2		: 1 :	1

Thus this hypothesis, which was first suggested by Mr. W. J. Spillman, accounts for the occasional appearance of black hen chickens among Barred Rock fowl. But it does more. It says that the progeny of barred cocks, which happen to be hybrids, and barred hens, which must be hybrids, should consist of equal numbers of cocks and hens, and, while all the former should be barred, half the latter should be barred, the other half non-barred. Professor Castle of Harvard tells us in his "Heredity in Relation to Evolution and Animal Breeding" that in all such matings the results are as expected.

But the hypothesis has been tested by two other matings. Barred cocks which are known to breed true can be mated with non-barred hens, and non-barred cocks can be mated with barred hens. These matings should produce as follows:

Barred cocks		Non-barred hens		Barred cocks	Barred hens
MM BB	x x	M [F] b [b]	should produce	MM B b	M [F] B [b]
				1 :	1

Non-barred cocks		Barred hens		Barred cocks	Non-barred hens
MM b b	x x	M [F] B [b]	should produce	MM B b	M [F] b [b]
				1 :	1

For, in the first case, both sexes of chickens must get B from their sires and be barred, while, in the second case, the cocks must get B from their dams and be barred, but the hens must get b from their sires and, having a second b factor tied to their F factor, must be non-barred.

Dr. Raymond Pearl had both these matings made. Barred Plymouth Rock cocks were mated with Cornish Indian Game hens, which are black and non-barred. The progeny consisted of 60 cocks and 60 hens, all barred. Cornish Indian Game cocks were mated with Plymouth Rock hens, and the progeny consisted of 95 cocks, all barred, and 96 hens, all non-barred.

Thus this hypothesis accounts for the equality of the sexes and for certain characters being carried by one sex only.

Before going farther, it may be suggested as obvious that, when all the males in a set of progeny carry a dominant character and half the females carry that character, the other half its recessive, the factor for that recessive character is tied to the female factor. On the other hand, when all the females carry the dominant character and half the males carry that character, the other half its recessive, the factor for the dominant character is tied to the female factor. Even if no accurate count has been made but it has been observed that, without exception, the whole of one sex always carries the dominant character, while some of the other sex carry the dominant, as the Plymouth Rocks were observed to do, some the recessive, it may be taken that these rules hold.

But, among fowl, there are other factors coupled with that for femaleness. There are other breeds than the Plymouth Rocks with the same basal colour, black, but with different barring patterns. These are usually described as " silver " breeds. There are also breeds with another basal colour, buff or gold, and different barring patterns. These are usually described as " golden " breeds. In Belgium, there are two similarly barred varieties of fowl, the Campines. When silver cocks are mated with gold hens, the progeny are all silvers. Thus, black is dominant to buff or gold. But when gold cocks are mated with silver hens, the cocks are all silvers, the hens all golds. Therefore, since the dominant silver factor the hens carried is transmitted to their sons only, the gold factor they carried is tied to their female factor.

Still another tied factor is revealed by these Belgian fowl. In both varieties both sexes are barred, but not equally. While the hackle, rump, and tail feathers are always barred in the hens, the same feathers are not often barred in the cocks. Male chickens barred like the hens are occasionally hatched, but are not retained by the breeders. Since the hens are always barred on these feathers, but the cocks are not, it is obvious that the hens carry a barring and a non-barring factor, that the barring factor is dominant, and, since it is not handed on to the male chickens, that it is tied to the female factor. It is obvious, too, that the cocks occasionally thrown with barring on the hackle, rump, and tail feathers must be the sons of hens carrying a second barring factor.

This hypothesis as to the factors carried usually by Campine fowl was tested by the experience of English breeders, who imported both varieties from Belgium a quarter of a century ago. Preferring cocks which were completely barred—that is, barred on the hackle, rump, and tail feathers, as well as elsewhere—they retained those that were so thrown and bred from them. Mated with ordinary Campine hens, these cocks should produce only completely barred daughters, but both completely and incompletely barred sons. Thus, putting C for barring on hackle, rump, and tail feathers,

MM C c	x	M [F] c [C]

should produce

MM C c	MM c c	M [F] C [C]	M [F] c [C]

This was the result among the stock belonging to the Rev. E. Lewis Jones.

And when a cock has been bred and found which is pure for the factor C, his progeny of both sexes will all be completely barred. Mr. Jones found such a cock, and his progeny consisted of 6 completely barred cocks and 6 completely barred hens.

Thus among poultry three factors coupled with femaleness are demonstrated, together with three pairs of untied factors operating alongside them, and the factors which may be carried by the hens in a population in which all these factors are operating are:

		M	F
B	or	b	b
Bl	or	g	g
C	or	c	C

Nearly twenty years ago, Dr. Raymond Pearl found still another factor coupled with the female factor, and, at the same time, made a discovery of great economic importance. From 1898 to 1908, the Agricultural Experiment Station at Orono in Maine was engaged in the attempt to improve the laying capacity of its Barred Rock poultry. Relying on the theory that this could be done by breeding only from the best laying hens and their progeny, the hens were divided into two sections, the good layers in one, the poor in another. Sons of the best laying hens only were used in both sections, and pullets hatched in either section were moved from that in which they had been hatched so soon as their performances showed them to belong to the other. Yet, after ten years, the pullets hatched in the section with good hens laid no better than those laid in the section with bad. The proportions of good and bad layers produced in each section were about the same. No simpler experiment could have been devised, for the two sections differed in one point only: the one in containing good hens, the other in containing bad: yet the result was the same in both. Obviously, improvement is not to be attained by simply selecting good laying hens.

In 1908 the problem was placed in Dr. Pearl's hands, and his solution, with all the essential data, is to be found in Bulletins 166, 192, and 205 of the Maine Agricultural Experiment Station.

Problems in animal products are surrounded with many difficulties, not the least of which is the collection and orderly arrangement of the necessary data. Animals may vary in food supply, health, and comfort, and, accordingly, in productive activity, and much information has to be gathered about normal production before any inferences can be drawn and before abnormal results can be identified and treated with fairness and good judgment. Besides, as a rule, animals have usually passed a considerable portion of their lifetime before their rate of production is revealed, and, in the meantime, many accidents and disturbing causes may have intervened.

Happily, Dr. Pearl discovered a method of determining the hen's egg-laying capacity soon after she had begun to lay, and, by this, decreasing not only the necessary statistical labour but also the chances of the results being upset by disturbing causes. He found that hens fall into three grades: one laying over 30 eggs in their first winter season, another laying under 30, and still another laying none at all; and he found also that, in their subsequent productivity, hens remain in the grades in which they have begun. Dr. Pearl's dividing figure (30) must not, of course, be taken as absolute, but as movable in some degree, according to circumstances.

When Dr. Pearl's discovery became known on this side, Miss Murphy, of the Munster Institute, Cork,[1] confirmed it, but expressed it in a way which is perhaps more useful; which, at any rate, can be useful sooner, for it indicates the hen's grade a week or two after she has begun to lay. Miss Murphy found Dr. Pearl's three grades, but observed that, if they are spring-hatched, the first grade pullets begin to lay early in winter—before winter even—and lay about five eggs a week; that the second grade pullets either begin laying at the same time, but lay only half as many eggs, or begin later and lay at a higher rate; and that the third grade ones lay no winter eggs at all, or just a very few towards the end of winter. The following table shows the numbers of eggs laid per week, during the three winter months, December, 1913, and January and February, 1914, by eight typical hens belonging to each of these three grades. The total eggs laid by each hen during the winter and throughout the year, from November to the end of the following October, are also shown in the table.

Hens' Numbers.	*Weeks.*													*Eggs laid during Winter.*	*Eggs laid throughout the Year.*
	1	2	3	4	5	6	7	8	9	10	11	12	13		
48	—	—	—	—	2	2	5	4	4	7	6	6	5	41	200
235	—	4	6	5	5	6	5	5	5	5	5	5	7	63	199
50	—	1	6	4	5	4	6	4	4	4	5	4	4	51	203
158	5	5	5	5	4	5	5	4	5	4	5	5	4	62	202
53	—	—	—	3	5	5	7	6	6	5	5	6	7	55	218
51	—	—	3	6	4	6	6	5	5	6	5	5	7	58	209
9	6	5	5	5	5	4	5	4	5	4	5	5	4	62	209
176	6	6	6	5	5	5	5	5	5	5	4	6	1	64	208
58	1	2	4	3	4	4	—	—	—	—	—	—	—	18	96
163	—	1	3	3	3	3	1	—	—	—	3	3	2	22	99
204	—	—	—	—	—	—	—	2	5	6	6	1	—	20	92

[1] Now Mrs. Tom Newman, and still interested in poultry.

Hens' Numbers.	*Weeks.* 1	2	3	4	5	6	7	8	9	10	11	12	13	*Eggs laid during Winter.*	*Eggs laid throughout the Year.*
131	—	—	—	—	—	—	—	—	—	—	2	4	4	10	98
43	—	—	—	—	—	—	—	—	—	5	5	7	5	22	93
172	—	—	—	—	—	—	—	2	4	—	4	4	3	17	98
78	—	—	—	—	—	—	—	—	—	—	5	5	6	16	96
253	—	—	—	—	2	6	5	5	3	3	4	3	3	34	98
57	—	—	—	—	—	—	—	1	1	1	—	1	3	7	43
105	—	—	—	—	—	—	—	—	—	—	—	—	—	0	49
149	—	—	—	—	—	—	—	—	—	—	—	—	3	3	43
87	—	—	—	—	—	—	—	—	—	—	—	—	—	0	43
173	—	—	—	—	—	—	—	—	—	—	—	—	—	0	60
170	—	—	—	—	—	—	—	—	—	—	—	—	—	0	39
155	—	—	—	—	—	—	—	—	—	—	—	—	—	0	50
77	—	—	—	—	—	—	—	—	—	—	—	—	—	0	56

The outstanding feature of the ten years' experience at Orono was that, though they may be good layers and, therefore, must carry a factor, or factors, for good laying, good laying hens cannot hand on this factor, or factors, to their daughters. The factor, or factors, for poor egg laying must, therefore, be tied to that for femaleness, and must be recessive to a factor, or factors, for good laying carried by the cocks and transmitted by them to their daughters. If the tied factor were a dominant, all the daughters of all good hens would be good layers. If there be only one pair of factors, say X and x, then the following combinations should be carried:

By the Cocks.			*By the Hens.*	
MM XX	MM Xx	MM xx	M | F X | x	M | F X | x

But, since there are three grades of hens, there must be more than one pair of factors.

The first suggestion is that there are three free factors which are polygamous. If we call the third factor Y, without considering, meantime, whether or not it be dominant or recessive to X, then the following combinations should be formed:

By the Cocks.						*By the Hens.*					
MM XX	MM XY	MM Xx	MM YY	MM Yx	MM xx	M X	F x	M Y	F x	M x	F x

But, though there are just the three grades of hens, there are, judging from the assemblages of progeny they produce, more than six different combinations of factors carried among the cocks. Thus there must be more than three factors.

A glance at the numbers of eggs laid by the middle grade hens at the Munster Institute suggests another theory. These hens are of two kinds: one beginning to lay early in winter at a lower rate and another beginning to lay later at a higher rate. Thus there may be four groups of hens, and, if a factor which either of these two groups carries be dominant to a recessive carried by hens laying no winter eggs, then, under ordinary circumstances, the usual two-pair set should be produced:

X Y	X y	x Y	x y
Over 30 winter eggs.	Under 30 winter eggs.		No winter eggs.

But, with the tied and the untied factors operating, the hens should carry six different combinations of factors, the cocks nine, as follows:

The Hens.

	1		2		3		4		5		6	
	M	F	M	F	M	F	M	F	M	F	M	F
	X	x	X	x	X	x	x	x	x	x	x	x
	Y	Y	Y	y	y	y	Y	Y	Y	y	y	y
	Over 30 eggs.				Under 30 eggs.						No winter eggs.	

The Cocks.

1	2	3	4	5	6	7	8	9
MM	MM	MM	MM	MM	MM	MM	MM	MM
XX	XX	XX	Xx	Xx	Xx	xx	xx	xx
YY	Yy	yy	YY	Yy	yy	YY	Yy	yy

Unfortunately, no observations have been made by which the suggested division among the middle grade hens could be tested, but, since Dr. Pearl put forward the same theory, minus the suggestion, the suggestion may be neglected, not necessarily with regret, since it may have helped to make a difficult problem easier, and proceed to the proof, which is parallel to that adopted with the horse and cattle colours. *If there are nine* different combinations of factors among the cocks and six among the hens, then, in flocks containing all kinds of hens, the nine different kinds of cocks should leave nine different assemblages of daughters, as on p. 96.

The table on p. 96 shows the progeny of 28 cocks mated with different kinds of hens and that at least eight different assemblages of pullets were produced. No cock of variety 7, $\begin{matrix}\text{MM,}\\ \text{xx}\\ \text{YY}\end{matrix}$ seems to have been used. Figures which are not in accordance with expectation are enclosed within brackets. The figure $\frac{1}{2}$ is set down several times. This indicates hens which laid 30 winter eggs exactly. They are placed in two grades.

KINDS OF PULLETS EXPECTED FROM ALL POSSIBLE MATINGS.

	Dams.																	
	+30						−30									0		
Sires	M F X x Y Y			M F X x Y y			M F X x y y			M F x x Y Y			M F x x Y y			M F x x y y		
	Daughters.																	
	+30	−30	0	+30	−30	0	+30	−30	0	+30	−30	0	+30	−30	0	+30	−30	0
1. MM XX YY	8[1]	–	–	8	–	–	8	–	–	8	–	–	8	–	–	8	–	–
2. MM XX Yy	8	–	–	6	2	–	4	4	–	8	–	–	6	2	–	4	4	–
3. Mm XX yy	8	–	–	4	4	–	–	8	–	8	–	–	4	4	–	–	8	–
4. MM Xx YY	4	4	–	4	4	–	4	4	–	4	4	–	4	4	–	4	4	–
5. MM Xx Yy	4	4	–	3	4	1	2	4	2	4	4	–	3	4	1	2	4	2
6. MM Xx yy	4	4	–	2	4	2	–	4	4	4	4	–	2	4	2	–	4	4
7. MM xx YY	–	8	–	–	8	–	–	8	–	–	8	–	–	8	–	–	8	–
8. MM xx Yy	–	8	–	–	6	2	–	4	4	–	8	–	–	6	2	–	4	4
9. MM xx yy	–	8	–	–	4	4	–	–	8	–	8	–	–	4	4	–	–	8

[1] The figure 8 means "all," because the proportions in other cases are brought to a standard total of 8.

With such close agreement between expectation and results—the disturbances to which living animals are liable being allowed for—there can be no doubt that Dr. Pearl's hypothesis is established. Another factor is found to be coupled with that for femaleness, and, at the same time, two factors are found whose effects, when acting separately, are similar, but, when acting together, cumulative. Thus the possible combinations of factors in a population of hens on which the factors we have been discussing are operating may be represented thus, when B=barred, b=unbarred, Bl=black, g=buff or gold, C=barred on hackle, rump, and tail feathers, c=non-barred on these feathers, X=30 winter eggs, x=no winter eggs:

		M	F
B	or	b	b
Bl	or	g	g
C	or	c	C
X	or	x	x

But it must not be assumed that factors are tied to the female factor only. While Professor Morgan of Columbia University was experimenting with the small vinegar fly, *Drosophila melanogaster*, which usually has red eyes, a male was bred which had white eyes. This male was mated with normal females, and their hybrids had all red eyes. Therefore, red is dominant to white. But, when the hybrids were bred from, their progeny consisted of equal numbers of males and females, and half the males had white eyes. This mating, with its result, is parallel with that in which hybrid Barred Rock fowl produced non-barred black chickens, excepting that the black chickens were females, while these white-eyed flies are males. Obviously, the factor for white eye is tied to the male, not to the female factor,

KINDS OF PULLETS OBTAINED FROM ALL POSSIBLE MATINGS.

Variety Indicated.	No.	Good Hens.						Medium Hens.									Poor Hens.		
		1			2			3			4			5			6		
Cocks.		M X | F x			M X | F x			M X | F x			M x | F x			M x | F x			M x | F x		
		Y Y			Y y			y y			Y Y			Y y			y y		
		gd.	mm.	pr.	gd.	mm.	pr.	gd.	mm.	pr.	gd.	mm.	pr.	gd.	mm.	pr.	gd.	mm.	pr.
(1) MM	550[1]	16½		½ (1)[2]	16½		½ (1)[2]	16½		½ (1)[2]	16½		½ (1)[2]	16½		½ (1)[2]			
XX																			
YY																			
(2) MM	65				7	1	(1)	2	3	0									
XX	68				13	5	(2)[4]												
Y y																			
(3) MM	553	15	0	0	6	9	0				4	0	0						
XX	567	12	(2)[5]	0	7½	9½	0	(1½)	3½	0									
y y	562	8	0	0	5	6	0												
	552	11½	½	0	17	15	(2)[6]							2	1	0			
	554	8	0	0	12	12	(1)[7]	0	3	0				1	3	0			
	564				9	10	(2)[8]	0	2	0				2	2	0			
	58				10	13	(1)[9]	0	5	0									
	573	4	0	0	4½	6½	0							2	1	(1)[11]			
	563	18	(1)[10]	0	11	11	(1)[1]												
	56	7	0	0				0	3	0				9	4	0			
	D31	27½	(2½)[14]	0	10½	11½	0				5	0	(1)[15]	14	15	(1)[15]			
	559										5	(1)[12]	0	18	17	(2)[12]			
(4) MM	32				4	3	0												
X x	57	2	1	0										4	3	0			
YY	17													3	3	0			
	70	4	5	0										2	1	0			

(5)																			
MM	569	2	0	0	5½	6½	1	2	6	3	3	3	0						
X x	566	9	6	0	4	8	2												
Y y	D35				3	5	1				2	2	0	2	5	0			
	556	10½	10½	0	8½	10½	4												
(6)																			
MM	26				2½	9½	0				6	6	0						
X x																			
y y																			
(7)																			
MM																			
x x																			
YY																			
(8)																			
MM	558				(4)[18]	14	2				(1)[16]	9	0	0	8	4			
x x	529	(5)[13]	12	0	(1)[13]	1	1	(1)[13]	3	2									
Y y																			
(9)																			
MM	578	0	3	0							(1)	4	0	(1)[17]	9	8	0	0	4
x x	557	0	17	0							0	19	0						
y y																			

1 No. 550 was mated with both good and medium hens, but, as the progeny from each were not separated, they are entered twice over as above.

2 This pullet was abnormal, but with clear signs that she was of the good grade.

4 One showed by later performances that she was of a higher grade; the other was pathological.

5 One of these laid twenty-eight winter eggs, just on the critical number.

6 Unquestionably belong to a higher grade, but neither was bred from.

7 Was a late bird and pathological.

8 Their spring performances showed them to belong to the class higher.

9 Pathological.

10 Neither was bred form.

11 Was a June hatched bird and not bred from.

12 All late hatched.

13 All shown, by after performances, to belong to the class below.

14 One of the pullets in 2½ laid under thirty eggs. The embryos all died during incubation.

15 One of these pullets was pathological.

16 This hen showed, by her progeny, that she was of medium grade.

17 "Somatic fluctuations."

18 To account for these four exceptions, Dr. Pearl suggests "intrazygotic influence," which means that they may have been influenced by the fact that their mothers carried X.

and the male is the hybrid. If that be so, then, mated with the female hybrids already produced, this white-eyed male should produce equal numbers of males and females, with equal numbers of red-eyed and white-eyed individuals in both sexes:

White-eyed Male.	x	*Hybrid Female.*		*Males.*		*Females.*	
				Red.	*White.*	*Red.*	*White.*
M F		FF	should produce	M F	M F	FF	FF
w w		wR		w R	w w	wR	ww

Also, with red-eyed males, which are all hybrids, white-eyed females should produce equal numbers of red eyes and white eyes, but all the red eyes should be females, all the white eyes males, thus:

Red-eyed Male.	x	*White-eyed Female.*		*Red-eyed Females.*	*White-eyed Males.*
M F		FF	should produce	FF	M F
w R		ww		wR	w w

Morgan's own account of his experiments has not been seen, but Castle, in his "Genetics and Eugenics," 1916, says that these predictions were fulfilled.

Other pairs of factors were found, with the recessive similarly tied to maleness, as, for instance, yellow body recessive to grey body, black recessive to grey, and vestigial wings recessive to long wings. When flies carrying any one of these recessives were mated with others carrying that recessive's dominant, the results in the next and succeeding generations were such as are to be expected if the recessive be tied to maleness. But, when flies carrying two of these recessives were mated with flies carrying the two corresponding dominants, the results were not as is to be expected.

Females which were hybrid for both red eye and grey body were produced, probably by mating white-eyed, yellow-bodied males with pure red-eyed, grey-bodied females. Then white-eyed, yellow-bodied males were mated with these hybrid females. In other words, white-eyed, yellow-bodied males were mated with their hybrid daughters. By this mating, equal numbers of four different kinds of males and females should have been produced. Putting w for white, R for red, y for yellow, and G for grey:

M	F		FF
w	w	x	wR
y	y		yG

Should have produced:

Males.								*Females.*			
M	F	M	F	M	F	M	F	FF	FF	FF	FF
w	w	w	w	w	R	w	R	ww	ww	wR	wR
y	y	y	G	y	y	y	G	yy	yG	yy	yG

white eye, yellow body	white eye, grey body	red eye, yellow body	red eye, grey body	white eye, yellow body	white eye, grey body	red eye, yellow body	red eye, grey body
1 :	1 :	1 :	1 :	1 :	1 :	1 :	1

Instead, they produced in both sexes:

White eyes, yellow bodies.	*White eyes, grey bodies.*	*Red eyes, yellow bodies.*	*Red eyes, grey bodies.*
49·25 per cent.	0·75 per cent.	0·75 per cent.	49·25 per cent.

Different, yet in one case approximately similar, results were got by Professors Bateson and Punnett in their experiments with sweet peas. One of the plants, Painted Lady, found among those with coloured flowers produced by crossing two plants with colourless flowers, was crossed with another plant called Duke of Westminster. The differences between the two were: Painted Lady was red, and the upper part of the flower—the standard—was erect; while Duke of Westminster was purple, with a hooded standard. Their hybrids had purple flowers and erect standards. Therefore, purple is dominant to red, and erect standard to hooded. Their hybrids' progeny should have consisted of four kinds:

P E		P h		r E		r h
Purple erect		Purple hooded		Red erect		Red hooded
9	:	3	:	3	:	1

Instead, they consisted of 2 erect purples: 1 hooded purple: 1 erect red. No hooded red was produced; and, further, the hooded purples and erect reds bred true, while the erect purples continued to breed like the hybrids.

Professor Punnett's explanation of the phenomena is: "On the assumption that there exists a repulsion between the factors for erect standard and blue (*i.e.*, the factor which overrides red and makes it purple) in a plant which is heterozygous (*i.e.*, hybrid) for both, this peculiar case receives a simple explanation." That is to say, two hybrids carry the factors:

......................P P......................
......................r r......................

......................E E......................
......................h h......................

In the distribution of the first pair, the following combinations are formed:

	PP		Pr rP		rr
i.e.	PP		Pr		rr
	1	:	2	:	1

But, because E and P refuse to keep company, E must go with r and h with P, r and h get no chance of combining, and the combinations formed by the two pairs of factors are:

PP	Pr	rr
hh	hE	EE
Hooded purple	Erect purple	Erect red
1 :	2 :	1

A similar result was got when plants having purple flowers and round pollen were crossed with others having red flowers and long pollen. The hybrids had purple flowers and long pollen. Thus purple is still dominant to red, and long pollen is dominant to round. The hybrids' *progeny should have consisted* of the four kinds, putting L for long pollen and o for round:

P	P	r	r
L	o	L	o
Purple long	Purple round	Red long	Red round
9 :	3 :	3 :	1

Instead, they consisted of purple long, purple round, and red long in the proportion 2 : 1 : 1. No red flowers with round pollen were produced.

The factors offered by the hybrids are:

......................P	P......................
......................r	r......................
......................L	L......................
......................o	o......................

In the distribution of the first pair, the following combinations are formed:

PP	Pr	rr
1 :	2 :	1

But because L and P refuse to be distributed together, L goes with r and P with o, r and o get no chance of combining, and the combinations formed by the two pairs of factors are:

PP oo	Pr oL	rr LL
1 :	2 :	1
Purple round	Purple long	Red long

It will be noticed that, in both these examples, each of the original parents carried only one of the repelling factors. In the first, the purple flower with hooded standard carried P, the red flower with erect standard carried E; in the second, the purple flower with round seeds carried P, the red flower with long seeds carried L.

An experiment was made in which one original parent carried both the repelling factors, the other neither. Plants having purple flowers and long seeds were crossed with plants having red flowers and round seeds. Their hybrids should carry the factors $\frac{P\ r}{L\ o}$, and the hybrids' progeny should consist of the four groups:

P L	P o	r L	r o
Purple flower, long pollen	Purple flower, round pollen	Red flower, long pollen	Red flower, round pollen
9 :	3 :	3 :	1

Instead, however, they consisted of these four kinds, but in a proportion approximating to:

177 : 15 : 15 : 49

The purples are still to the reds and the long pollens to the rounds in the normal proportion 3 : 1, but the combinations are not as they should have been had the factors been distributed in the normal manner. Their distribution has been interfered with.

Different hypotheses have been set up to account for these irregular phenomena. Morgan's may be the soundest. It is that the factors (which the Americans call "genes") are housed upon four or five pairs of almost infinitely small rods and dots lying within the nucleus of the reproductive cells. These rods and dots are called chromosomes (coloured bodies), because they take on the laboratory worker's stains readily. The theory is, further, that different factors are housed upon different chromosomes, some upon one, others upon others, but that some factors—there may be two or more—when they become housed together, are unwilling to separate again, and so, when one factor is handed on by a parent to its progeny, the other factors which are unwilling to separate from it are also handed on at the same time. Thus, when the Barred Rock hen hands on her factor for femaleness to her daughter, she hands on, at the same time, a factor for non-barring. Thus also, when the white-eyed vinegar fly hands on to his son his factor for maleness, he hands on, at the same time, a factor for white eye. On this hypothesis, if a sufficient number of the sons of a white-eyed, grey-bodied vinegar fly were to become possessed of a yellow-body factor and this factor were housed on the same rod as the factors for maleness and white eye and become inseparable from these two factors, their progeny, with hybrid, red-eyed, grey-bodied females should be:

White-eyed, yellow-bodied.	*White-eyed, grey-bodied.*	*Red-eyed, yellow-bodied.*	*Red-eyed, grey-bodied.*
49·25 per cent.	0·75 per cent.	0·75 per cent.	49·25 per cent.

The hypothesis set up to explain the unexpected result produced when a pea bearing one dominant was mated with one bearing another was that the factors for the two dominant characters repelled each other. The result might also be explained on the hypothesis that the factor for one of the dominant characters had become tied to that for the recessive character on the same plant, If, for instance, the factors for purple flower, P, and hooded standard, h, carried by Duke of Westminster, had become tied, while those for red flower r, and erect standard, E, carried by Painted Lady, remained free, the factors carried by parents, hybrids, and hybrids' progeny would be as follows:

Parents.				*Hybrids' progeny.*		
Duke of Westminster.		*Painted Lady.*	*Hybrids.*			
P/h P/h	x	rr EE	P/h r/E	P/h P/h	P/h r/E r/E P/h	rr EE
				Purple hooded	Purple erect	Red erect
				1 :	2 :	1

With regard to the experiment in which the two dominants were carried by one parent and the two recessives by another, and the hybrids' progeny consisted of four kinds in the proportion 177 : 15 : 15 : 49, Professor Punnett remarks: "It will be noticed that in the whole family the purples are to the reds as 3 : 1, and the longs are also three times as numerous as the rounds. The peculiarity of the case lies in the distribution of these two characters" (*i.e.*, P and L) "with regard to one another. In some way or other the factors for blue" (*i.e.*, purple) "and for long pollen become linked together in the cell divisions that give rise to the gametes" (*i.e.*, the sex cells), "but the linking is not complete. This holds good for all the four cases[1] in which repulsion between the factors occurs when one of the two factors is introduced by each of the parents. *When both the factors are brought into the cross by the same parent, we get coupling between them instead of repulsion.*"

Professor Morgan's hypothesis would suggest that, in some proportion of the parent plants having red flowers and round pollen, the factors for these two characters had become tied, and these plants, with the purple, long-pollened plants, had produced hybrids carrying the characters $\begin{array}{c|c|}P & r \\ L & o\end{array}$, while, in the rest of the parent plants having red flowers and round pollen, no tying of factors had taken place, and with the purple, long-pollened parents, they had produced hybrids carrying the same characters untied. The progeny of the former of these two kinds of hybrids should consist of 3 plants having purple flowers and long pollen to 1 having red flowers and round pollen, while that of the second kind should consist of 9 plants having purple flowers and long pollen to 3 having purple flowers and round pollen, to 3 having red flowers and long pollen to 1 having red flowers and round pollen. Then, if 256 hybrids' progeny were produced, half of them by the first kind of hybrid, the other half by the second, the numbers and kinds produced should be:

	purple flower, long pollen.	*purple flower, round pollen.*	*red flower, long pollen.*	*red flower, round pollen.*
By the first hybrid	96	—	—	32
By the second hybrid	72	24	24	8
Totals	168	24	24	40

[1] There were other experiments in which one parent carried one dominant, the other parent another.

These totals are not far from Bateson and Punnett's, but, since the numbers in the first and last groups are raised, while those in the middle groups are depressed, as the proportion of the progeny of the first kind of hybrid increases, the totals can be brought nearer the experimental results by increasing the first kind of hybrid's progeny. If they are increased to 176, that is eleven-sixteenths of 256, the progeny of the two kinds of hybrids become:

	purple flower, long pollen.	*purple flower, round pollen.*	*red flower, long pollen.*	*red flower, round pollen.*
By the first hybrid	132	—	—	44
By the second hybrid	45	15	15	5
Totals	177	15	15	49

Presumably, therefore, the factors for red flowers and round pollen became tied in nearly 70 per cent. of the crosses between sweet peas carrying two dominant characters and peas carrying two recessives.

X

CROP AND ANIMAL PRODUCTS

We now come to that part of the work which is economically most important, but, as yet, cannot be subjected to accurate treatment. Dr. Pearl was fortunate in discovering that there are three grades in egg laying and in identifying the factors which produce them. But in other animal products—and in crop yields also—there are many more grades than three; and, till a set of animals breeding true to one grade or another has been found, it is unlikely that the different grades will be discovered and the strengths of the factors which produce them identified. This chapter contains, therefore, a short indication of how crop and animal yields were improved without, and suggests how they might be further improved with, the help of Mendel's discovery.

Patrick Shirreff, an East Lothian farmer, perhaps the most successful of all pre-Mendelian crop improvers, tells, in his autobiography, how his work was begun: "When walking over a field of wheat on the farm of Mungoswells, in the county of Haddington, in the spring of 1819, a green, spreading plant attracted my notice, the crop then looking miserable from the effects of a severe winter; and next day measures were taken to invigorate its growth by removing the surrounding vegetation and supplying manure to the roots. In the course of the summer, several stalks were cut down by hares; but notwithstanding this loss to the plant, sixty-three ears were gathered from it at harvest, yielding

2473 grains, which were dibbled in the following autumn at wide intervals. For the two succeeding seasons the accumulating produce was sown broadcast, and the fourth harvest of the original plant amounted to about 42 qr. of grain fit for seed; and proving to be a new variety, it was named Mungoswells wheat."

How, where, and when this new wheat had originated will never be known. It was undoubtedly a "natural cross," the descendant of innumerable earlier natural crosses, and Shirreff had the eye to see it and the sense to accumulate a stock of it apart from all other wheats. It was not the first grain so discovered. The "potato" oat was discovered in a potato field in Cumberland in 1788, and, till shortly after this time, when Knight, a noted horticulturist, "readily obtained as many varieties as he wished by merely sowing the different kinds together," all new varieties of grain and other field crops must have been raised in some closely similar manner.

But Shirreff was not content with one new variety. For thirty or forty years he persisted in hunting for new varieties in his own and his neighbours' fields, accumulating stocks, testing them for yield, and putting them on the market. In these thirty years he gave the world many new varieties of wheats and oats, some of which, under their original or new names, are still in cultivation. Then came the tragedy. He began crossing, and, as we should now expect, his crosses did not breed true, and he became bewildered among their descendants. In his autobiography, he gives a reason for his success with natural or, as they are now called, single-ear selections, and, inferentially, for his lack of success with crosses: "My selections have chiefly been from natural sorts, which soon show their propensities, and often prove constant, having in all probability undergone reproduction before being selected. . . . Sports may be regarded as the gift of nature to man."

Most instructive of all, perhaps, is the work done at Svalöf, in Sweden. Sweden had been a grain-exporting country since 1840, but, about 1870, the effects of oversea competition began to be felt, and the remuneration for exported grain to decline. In 1886, thinking that the Swedish farmer's position would be bettered if he grew higher-yielding varieties, Herr Birger Belinder and a few of his neighbours near Svalöf established the Swedish Seed Association, whose purpose was to discover the best varieties of grain for Southern Sweden. Believing that the varieties they had been growing had declined in yield through the admixture of smaller-yielding varieties—through impurities—the society's work resolved itself into:

(*a*) Procuring good-yielding varieties from other countries.

(*b*) Finding the best-yielding native varieties.

(*c*) Growing these side by side and comparing their yields.

(*d*) Eliminating the poor varieties and propagating the good till a stock had been accumulated.

(*e*) Keeping the good varieties pure and purifying the impure.

(*f*) Distributing the good varieties among members of the association and other farmers.

The association acquired land at Svalöf and appointed a director to carry on the work. For ten or twelve years little was done beyond find, grow, and test different varieties for yield, and keep the best ones up to standard in purity. This last was done by roguing or culling such plants as differed from the bulk of the variety in size, length of straw, thickness of straw, length of head, shape of head, and so on; and by cleaning the seed and regulating its size by the riddle.

It was hoped that some varieties would be improved by all this care, but very little improvement was made. The roguing of growing plants unlike the bulk might raise the yield of the bulk, if these rogues were lower yielders than the bulk, but it would not do so necessarily because these plants differed from the bulk in certain physical vegetative characters. The riddling might eliminate small seeds, or large seeds, or both, but it need not increase the yield, unless these eliminated seeds were associated with small yields. Even in its most drastic use, which consists, say, in selecting the very largest plants, with the largest heads, and retaining only the largest grains, this method may bring about no improvement, for it may be that none of these characters is associated with large yield. Because large grains may give the young plant a better start, the yield of any pure variety may be raised for one year by sowing only the largest grains of the previous year, but it does not necessarily follow that the rise will be maintained unless the seed continue to be similarly selected.

It was observed very early at Svalöf that none of the varieties tried was absolutely pure, but that all included sub-varieties which were distinguishable from the bulk by slight botanical differences. At first, this was not thought to be important, but, when several plots which were known to be descended from single plants were found to be uniform and uniformity was thus shown to be attainable, it was decided that the method by which improvement had been sought would have to be modified, and only pure-breeding kinds submitted to investigation. Otherwise, no results could be relied on completely.

About this time, Professor Hjalmar Nilsson had become director, and he decided to adopt the single-ear method—Shirref's method—of selection and cultivation. By this method the descendants of a single plant are grown apart from all other similar plants till stock enough has been accumulated to tell whether the kind so selected is good or bad. About the same time the idea that botanical characters are indications of yield was abandoned at Svalöf, and the findings of the weighing machine only accepted.

Before 1900, a number of good-yielding varieties had been identified at Svalöf, nearly all of which were descended from imported varieties; none from single ears. It had been found that wheat yields were depressed by three main causes: severe winter weather, rust, and lodging: and that some varieties withstood these depressing causes better than others. The table on page 114 gives the yields of seven different varieties over six successive seasons, and shows how these varieties were affected by winter weather. These varieties were known to be so affected by 1900, but they were tested again over the years 1907 to 1912 to confirm the earlier knowledge. The yields are given in kilogrammes to the hectare, but may be read in pounds to the acre without altering the figures. In the last column, all the yields are reduced to a comparable base, with that of a native variety, Sammets wheat, standing at 100.

It will be observed that some of these varieties give large yields after a mild winter—1910, for instance—but fail when the winter has been severe, while others give smaller yields after a mild winter, but are much less affected by severe winters. Obviously, it should be possible, or, at any rate, an attempt should be made, to discover whether it be possible to mate a winter hard variety with a winter soft but high-yielding variety, and combine in their descendants the desirable characters carried by both parents. And it should be possible, by mating with these plants which withstood rust and lodging, to produce varieties which should withstand not only hard weather, but rust and lodging, in addition.

Variety.	*Kilogrammes per hectare.*						*Average.*	*Reduced to standard.*
	1907	1908	1909	1910	1911	1912		
Sammets wheat	2370	3310	2370	4140	3930	3440	3260	100·0
Strubes Squarehead	2540[1]	3540[2]	760[3]	5380	4490[1]	2710	3220	98·8
Stand Up ..	3170[1]	3660[2]	950[3]	5360	4740	3370[2]	3550	108·9
Extra Squarehead	2460	4030	2640	4500	—	—	3647	111·9
Danish Bore wheat ..	2760	3910	2900	4580	4210	4150	3752	115·1
Renodland Squarehead ..	2740	3580	3420	5220	4590	4180	3955	121·3
Grenadier II. ..	3110	4240[1]	2620[2]	4950	5110	3720[1]	3959	121·4

Crosses had been made before 1900, but, since the appointment, at that time, of Dr. Nilsson-Ehle, to take charge of the wheat and oat experiments, crosses have been made on the assumption that still higher-yielding varieties would be obtained by eliminating winter softness and the tendencies to lodging and rust from varieties which, but for one or more of these weaknesses, would have been high yielders. The details of Dr. Nilsson-Ehle's work, so far as we are now concerned, are to be found in his paper, "Berätelse öfver Förätlingsarbetena med Höstvete vid Svalöf, 1910-1912."

Two varieties mentioned in the table above, namely, Extra Squarehead, which was winter hard and rust resisting, and Grenadier II., which resisted lodging, were

[1] Slightly damaged by winter. [2] Fairly strongly damaged.
[3] Very strongly damaged

mated; and, when their true-breeding descendants which resisted winter, and rust, and lodging, had been identified, and the best yielders discovered, and stocks of these accumulated, in 1909, the new variety, Extra Squarehead II., was sent out to the farmers. The following table gives the average yield of this variety as compared with those of its parents and that of the native variety, Sammets wheat, over the years 1907 to 1912, excepting that the average for Extra Squarehead covers the years 1907 to 1910 only:

		Average.	*Reduced.*
Standard:	**Sammets wheat**	**3260**	**100·0**
Parents:	**Extra Squarehead**	**3647**	**111·9**
	Grenadier II.	**3959**	**121·4**
	Extra Squarehead II.	**4255**	**130·5**

Another cross gave a still higher yield. Among a native variety called Kotte wheat, a plant was found which was evidently a natural cross between Kotte and one or other of the imported varieties. With good yield, this plant combined strong winter resistance and exceptionally strong resistance to rust; but it was inclined to lodge, was late in ripening, and had grain of poor quality. Consequently, it was of no economic importance. It was crossed, however, with Grenadier II. —Extra Squarehead II. was not yet available—and, from among the descendants, a variety was selected of good quality, whose yield was even higher than that of Extra Squarehead II. When Professor Nilsson-Ehle's paper was published, this variety was still designated by a number only—0801—but it had been tested over a period of five years, and, if we set down the average yields of itself and its parents, together with similar figures for Extra Squarehead II. and its parents, we shall see the advance it made:

		Years tested.	Average.	Reduced.
Standard:	Sammets wheat	6	3260	100·0
Parents:	Extra Squarehead	4	3647	111·9
	Grenadier II.	6	3959	121·4
	Extra Squarehead II.	6	4255	130·5
Parents:	Kotte cross	—	—	—
	Grenadier II.	6	3959	121·4
	0801	5	4576	140·5

Nor is this the end, for, when Extra Squarehead II. became available, a descendant of the cross between it and a high-yielding Danish wheat, called Tystofte Smaawheat, gave a higher yield in 1912 than either parent. In the same year, another variety selected from the stock which had produced 0801, gave a higher yield than any. The following table gives the yield of these varieties for the one year, 1912. In the last column, the yields are reduced to the old basis, but represent one year's results only:

		Kilogrammes per hectare.	Reduced.
Parents:	Extra Squarehead II.	3950	130·5
	Tystofte Smaawheat	4350	143·7
	0860, the new variety	4750	154·5
	0801, the new selection[1]	4950	163·5

Thus by mating varieties which are high yielders, because of other factors of which nothing is known, and by eliminating the factors which make the plant non-resistant to winter, rust, and lodging, the Swedish farmer is now in possession of wheats which are about 50 per cent. better than their old varieties.

Success in almost similar measure was obtained by some of the older live-stock breeders, more especially by those who are generally described as the "original

[1] Afterwards named Swedish Iron?

improvers" of one or another breed. Their method was generally to select parents carrying the characters desired and breed with such as reproduced those characters. The first of these early breeders was Bakewell, who was born at Dishley, in Leicestershire, in 1726, and died there, in 1795. His chief successes were with cattle to produce beef and sheep to produce mutton. About 1760, after travelling up and down the country to discover which were the best cattle to produce beef, he added to the stock already on his farm a bull from Westmorland and several heifers from Warwickshire which were descended from stock raised near Burton-on-Trent. The ordinary breeder would have sent this bull away when his eldest daughters were rising three and he was four or five years old, but, because he could find no other bull to take his place, Bakewell kept this bull till he was at least seven or eight years old, and one of his sons was found fit to take his place. This son was also retained till one of his sons again was found fit to take his place; and this practice of selecting successive sires from his own stock was continued by Bakewell throughout his lifetime. A sire which left stock carrying the characters Bakewell desired them to carry was kept alive till a son was found which bred equally well or better. One of his sires was at least twelve or thirteen years old before being sent away. This meant that Bakewell's stock were very closely in-bred. To other breeders, this seemed wrong. It may have seemed wrong to Bakewell also, but, against that, he was breeding and using sires which bred what he desired: which bred true and produced younger stock which also bred true.

Bakewell's method is, perhaps, more clearly indicated by his practice with sheep. When his flock which, like his herd, started with the introduction of sheep from elsewhere, was established, other breeders wished to buy sires from him. But Bakewell would not sell sires; he would only let. Thus, though the lambs they produced belonged to other breeders, the sires still belonged to Bakewell, and those that bred the kind of stock Bakewell desired could be brought home again to Dishley. Thus Bakewell's stock, both cattle and sheep, were all in-bred; not necessarily on purpose, however, but as a consequence of his relying on proved and tested sires, which were only to be found among his own stock.

A more recent example comes from Denmark. The Danes began to keep milk records about half a century ago, and use the information so obtained to improve their milking stock. At first only the milk yield was recorded, but, when a simple method of determining the quantity of butter fat in the milk had been found, the quality of the milk was also recorded. Improvement was brought about by discarding the cows which gave low yields and milk of poor quality and selecting sires from among the sons of the best cows. It is not improbable that the former of these two methods had the more effect, because it increased the average yield and at the same time reduced the chances of inferior animals being bred.

It was soon found that certain sires left daughters which gave more milk, while others left daughters which gave better milk than their dams; and Mr. A. M. Christensen published two reports[1] to show how one sire, Lombjerge IV., with his sons and grandsons, had raised the milk yields in the herds in which they had been used, and another, Taurus IV., with his sons and grandsons, had raised the quality (that is, the fat content) of the milk. Both lines of sires had raised the yield, but the

[1] Tyreslagters Infledelse paa Afkommets Ydelse: vol. i., Lombjerge IV.; vol. ii., Taurus IV.

Taurus line had raised the quality also. The latter came to be called " butter " bulls.

When he heard of these butter bulls, Mr. Grut Hansen, of Kolle Kolle, ten or twelve miles north of Copenhagen, who was already one of the most successful breeders of Red Danish cattle, decided to have one of these butter bulls which had been proved to be such by the milk his daughters had produced. This meant that the bull could not be less than six or seven years old, and bulls were not usually kept alive till they reached this age. One was found, however, called Dan, a son of Taurus IV. and a cow whose milk, on the average of seven years, contained 4·16 per cent. of fat. Dan was used by Mr. Hansen till he was thirteen or fourteen years old, and was succeeded by another proved sire called Hermod, Hermod by another called Skjold. This carried Mr. Hansen on to 1914, when he fell into poor health and never recovered. When he died, he left his herd to his fellow-breeders of Red Danish cattle. Unfortunately, the writer of this volume has no knowledge of what has happened in the Kolle Kolle herd since 1914; but, by the use of these three butter bulls in succession, Mr. Hansen raised the average quantity of butter fat in the milk of his whole herd from about 3·4 per cent., when Dan was introduced, to about 4·2 per cent. in 1914. The following table will indicate how far each of these four sires was capable of raising the quality of the daughters' milk above that of the mothers':

Sires of daughters.	*Average percentage of fat in*	
	The mothers' milk.	*The daughters' milk.*
Taurus IV.	3·58	3·88
Dan	3·40	3·89
Hermod	3·80	4·21
Skjold	4·00	4·20

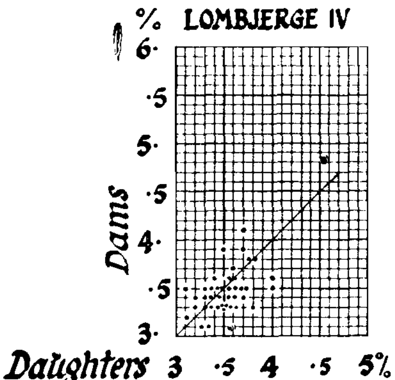
About the same time another Danish breeder, Count Ahlefeldt, of Tranekjaer, in Langeland, was endeavouring to raise the quality of his Red Danish cows' milk by crossing them with Jersey bulls. First the Red Danish cows were crossed by one Jersey sire, then their daughters were crossed by another. The percentages of butter fat in the Red Danish cows' milk and in that of their half-bred daughters and three-quarter-bred granddaughters were as follows:

	Red Danish.	*Half-bred Jersey.*	*Three-quarter Jersey.*
	3·07	3·52	4·66
	3·08	4·40	4·41
	3·15	3·85	4·55
	3·19	4·02	4·83
	3·30	3·64	4·36
	3·33	4·02	4·55
	3·35	3·66	4·67
	3·38	4·20	5·02
	3·41	3·85	4·52
	3·41	4·12	4·72
	3·41	4·04	4·58
	3·44	4·26	5·66
	3·55	4·48	4·88
	3·58	4·63	5·15
	(?)	4·50	5·41
Average:	3·33	4·08	4·80

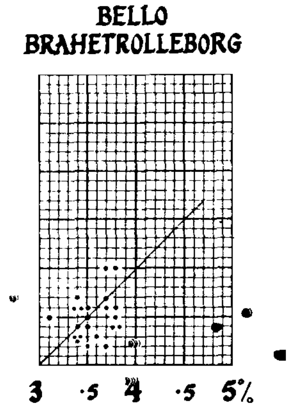
But though these examples show that the milk of a breed may be raised in quality by the continued use of "butter" bulls, just as the beef-producing capacities of many breeds were raised in Britain by the continued use of "beef" bulls, neither the Kolle Kolle nor the Tranekjaer figures gave any clear indication of the steps through which the fat content of the milk was raised. When these figures became known, the writer of this volume, assuming that there were two main grades of milk—Jersey milk, containing about 5 per cent., and other milk about 3·5 per cent. of butter fat—suggested that there were two main factors concerned in butter-fat production, namely, one producing about 5 per cent., and another about 3·5 per cent., with their hybrid producing an intermediate quality of about 4·3 per cent.; and that there were other factors having a small modifying effect upon these factors. But when the Kolle Kolle and other figures became known, it was obvious that the suggestion was not a good one, for it was found that the butter fat in milk may vary far more widely than was assumed—it may vary from about 2·5 per cent. to about 6 per cent.; possibly more widely still—and that there were not three main grades.

Before going farther, it may be well to say that no figures about milk yields, whether about quality or quantity, can be absolutely accurate. In any one year, the quantity of butter fat in a cow's milk may vary as much as 10 per cent. from that cow's true average. That is to say, a cow whose true average is about 4 per cent., may, in any one year, chiefly because of her physical condition and the length of the lactation period, give milk containing as much as 4·4 per cent. or as little as 3·6 per cent., of butter fat. But, if they be calculated from four or five years' yields, as most of these Danish averages are, the calculated averages cannot be very far from the true.

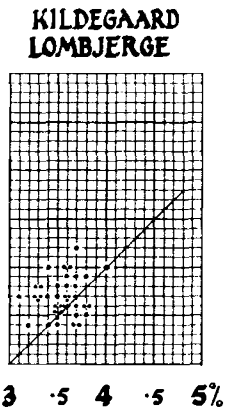
Some indication of the steps through which the milk fat was raised and of the different grades in milk quality may be obtained through the following diagrams. In the first nine, the quality of the milk given by the daughters of nine different sires is plotted, horizontally, against the quality of the milk given by these daughters' dams, perpendicularly. The first three sires are so-called "milk" bulls, the next four "butter" bulls, the



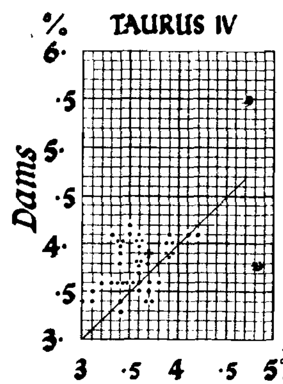
Dams' average = 3·51%
Daughters' average = 3·48%



Dams' average = 3·58%
Daughters' average = 3·5%

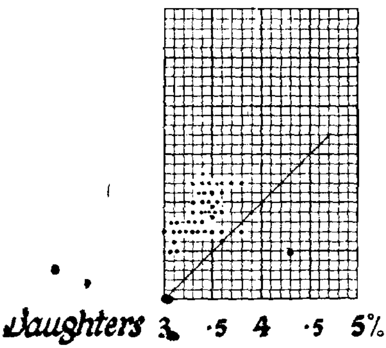


Dams' average = 3·55%
Daughters' average = 3·73%



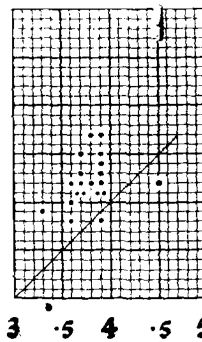
Dams' average = 3·58%
Daughters' average = 3·88%

DAN



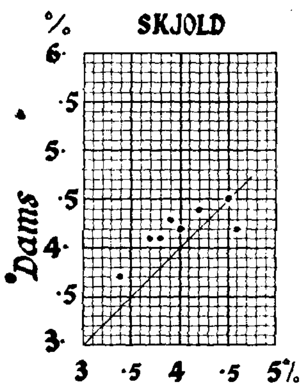
Dams' average = 3·4%
Daughters' average = 3·89%

HERMOD



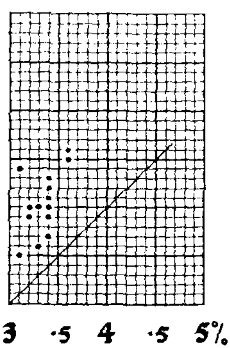
Dams' average = 3·8%
Daughters' average = 4·21%

SKJOLD



Dams' average = 4%
Daughters' average = 4·2%

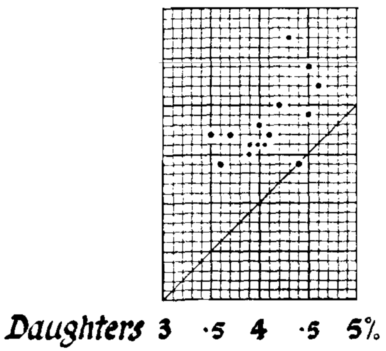
JERSEY No. 1



Dams' average = 3·33%
Daughters' average = 4·04%

last two Jerseys. It will be seen, by examining this diagram, that the third bull might have been called both a milk and a butter bull. In the tenth diagram (p. 125) the continuous line shows the numbers of cows giving different grades of milk among those mated with the first five Red Danish and the first Jersey sire, the dotted line the numbers giving different grades among the daughters of all but the first two bulls. That is to say,

JERSEY No. 2

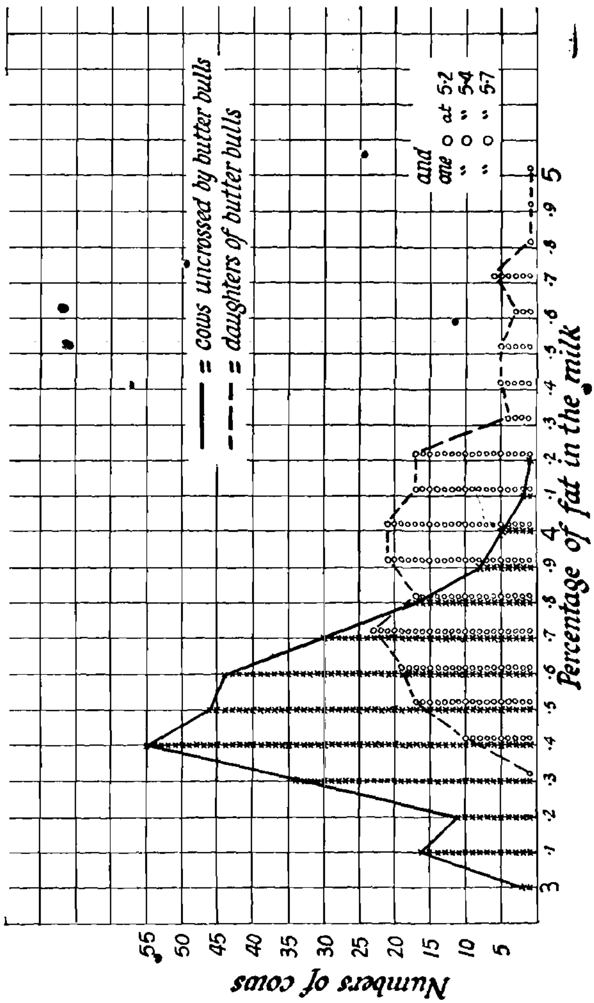


Dams' average =4·08%

Daughters' average =4·8%

the continuous line shows how many cows gave milk of one grade or another before they were crossed by butter bulls, the dotted line how many gave milk of one grade or another after their dams or their granddams had been crossed by butter bulls.

The last of these diagrams indicates, by its spread, that there are many grades in the quality of milk, and that the grades lie close to each other. There is obviously one near 3·1 per cent., and others near 3·4, 3·6, and 3·9 or 4·0; and, if the lowest grade be near 2·5, the highest


= cows uncrossed by butter bulls
= daughters of butter bulls
and
one o at 5·2
" o " 5·4
" o " 5·7
Percentage of fat in the milk
Numbers of cows
3 ·1 ·2 ·3 ·4 ·5 ·6 ·7 ·8 ·9 4 ·1 ·2 ·3 ·4 ·5 ·6 ·7 ·8 ·9 5
55 50 45 40 35 30 25 20 15 10 5

near 5·5, and the differences between each grade from 0·2 to 0·3 per cent., there must be from 10 to 15 different grades. The other nine diagrams also indicate a number of different grades. Judging by their lowest-grade daughters, Lombjerge IV. and Bello Brahetrolleborg indicate that there is a grade near 3·1 or 3·2 per cent.; and Kildegaard Lombjerge, Taurus IV., Dan, and the first Jersey bull that there is another near 3·4 or 3·5 per cent., while the second Jersey bull indicates that there is a grade near 4·5 per cent., and others between that figure and 5·5 per cent.

Fall (−) or rise (+) through	*Number of Daughters of*								
	Lombjerge IV.	*Bello Brahe-trolleborg.*	*Kilde-gaard Lombjerge.*	*Taurus IV.*	*Dan.*	*Hermod.*	*Skjold.*	*Jersey No. 1.*	*Jersey No. 2.*
Per Cent.									
−0·5	2	1	—	—	—	—	—	—	—
−0·4	1	2	—	—	—	—	1	—	—
−0·3	3	3	3	2	—	1	—	—	—
−0·2	8	—	3	2	—	—	—	—	—
−0·1	5	5	2	6	1	1	—	—	—
0·0	9	3	8	4	1	—	1	—	1
+0·1	6	1	8	6	1	—	—	—	—
+0·2	4	3	4	10	1	3	2	—	—
+0·3	—	2	3	2	3	1	2	2	—
+0·4	3	1	5	7	8	5	2	1	1
+0·5	—	—	3	2	12	2	—	1	—
+0·6	—	—	2	3	6	3	—	1	5
+0·7	—	—	—	1	7	—	—	3	1
+0·8	—	—	—	2	1	2	—	2	3
+0·9	—	—	—	—	2	1	—	2	1
+1·0	—	—	—	—	—	—	—	1	1
+1·1	—	—	—	—	—	—	—	—	—
+1·2	—	—	—	—	—	—	—	—	1
+1·3	—	—	—	—	—	—	—	1	—
+1·4	—	—	—	—	—	—	—	—	1

The nine first diagrams show that, though sometimes the dam's and the daughter's milks are of the same quality, there is generally a difference between the two; sometimes a rise, sometimes a fall. These differences indicate the various strengths of the different fat-producing factors separately or combined. If, for instance, a cow's milk contained, say, 3·5 per cent., and her daughter's 5 per cent. of butter fat, that rise might be brought about by the interchange of two factors, one of which was 1·5 per cent. stronger than the other, or by the displacement of several factors by others whose combined strength was 1·5 per cent. higher. The factors 2·0+1·0+0·5 may have been interchanged for 2·0+1·5+0·5, or for 2·5+1·5+1·0. The table on p. 126 shows how often and how far the quality of the milk of the daughters of these nine bulls fell below or rose above that of their dams.

We are now in a position to speculate—and till a stock of animals breeding true to one grade or another has been bred, we are very unlikely to be able to do more than speculate—as to what the strengths of the different factors are likely to be. We have seen that milk may contain from about 2·5 to 5·5 per cent. of butter fat, and that, including these extremes, there must be not less than ten to fifteen different grades, some of which lie very close to each other. But, if there are more than eight grades, there must be sixteen at least, which means four pairs of factors, and, when the four strongest factors are carried by an animal, her milk must contain about 5·5 per cent. of butter fat, when the four weakest are carried by an animal, her milk must contain about 2·5 per cent.; and with all the various possible combinations of the factors, the grades must vary between these limits. Let us assume that there are four pairs of factors, that the higher of each pair is the dominant, and that the individual pairs produce the following percentage quantities of butter fat:

$$\frac{2{\cdot}2}{{\cdot}9},\ \frac{1{\cdot}7}{{\cdot}7},\ \frac{1{\cdot}2}{{\cdot}5}\ \text{and}\ \frac{{\cdot}5}{{\cdot}3}$$

With these four pairs of factors operating, the sixteen following groups may be formed producing the following grades of milk:

				Grade of milk (per cent.).
2·2	**1·7**	**1·2**	**0·5**	5·6
2·2	**1·7**	**1·2**	0·3	5·4
2·2	**1·7**	0·5	**0·5**	4·9
2·2	0·7	**1·2**	**0·5**	4·6
0·9	**1·7**	**1·2**	**0·5**	4·3
2·2	**1·7**	0·5	0·3	4·7
2·2	0·7	**1·2**	0·3	4·4
0·9	**1·7**	**1·2**	0·3	4·1
2·2	0·7	0·5	**0·5**	3·9
0·9	**1·7**	0·5	**0·5**	3·6
0·9	0·7	**1·2**	**0·5**	3·3
2·2	0·7	0·5	0·3	3·7
0·9	**1·7**	0·5	0·3	3·4
0·9	0·7	**1·2**	0·3	3·1
0·9	0·7	0·5	**0·5**	2·6
0·9	0·7	0·5	0·3	2·4

This speculation may not be a true fit, but it is not a very bad fit for the phenomena as they are at present known. Till a group of animals breeding true to one grade or another has been bred, it may help towards a better understanding of the problem. Meantime, no better method of raising the quality of the milk produced by a breed of cattle can be suggested than that adopted by the Danes. Sires which have been proved to be butter bulls should be kept alive till nature ends their life, and young sires should be selected from among the progeny of sires leaving high-grade progeny and dams yielding high-grade milk or bearing high-grade progeny. The table on page 126a nd the diagrams on pages 122-124 indicate that a sire may be judged by his worst daughters as readily as by his best, for generally the higher the grade of his worst the higher the grade of his best.

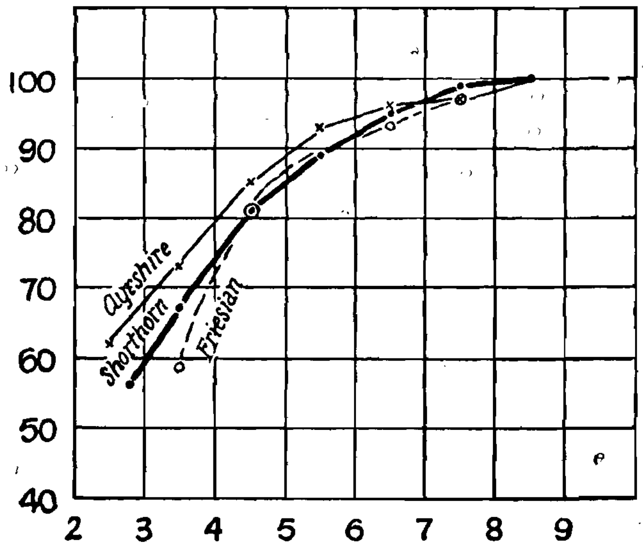
Like that concerned with its fat content, the work concerned with milk yield itself is still in the preliminary stages. When efforts were first made to trace the inheritance of milk yield with some degree of accuracy, it was found that yields not only vary greatly, but are liable to serious deviations from their own normal, and much work had to be done before these variations and deviations could be allowed for fairly.

The cow's annual yield rises, from her first lactation when she is a two-year-old or three-year-old, to her sixth or fifth, when she is an eight-year-old, remains near the eight-year-old level for a year or two, then falls again almost inversely as it rose. The rise is indicated in the following diagram, which is plotted from three different sets of cows: the dotted line from cows, chiefly Friesians, in Lord Rayleigh's herds in Essex,[1] the thick from cows exhibited at the London Dairy Show during ten or twelve years previous to 1912, and the thin line from Ayrshire cows whose yields were recorded during the years 1903 to 1907.[2] The yields of each set of cows are brought to the same level by multiplying them by the figures which bring those for eight-year-olds to 100. The diagram may be used to calculate a cow's probable yield at one age from her known yield at another. If, say, a Shorthorn cow's yield as a three-year-old be

[1] W. Gavin in the *Journal of Agricultural Science* for October, 1913, pp. 378 and 379.

[2] John Spier in "Report on Milk Records for Season 1908," p. 23.

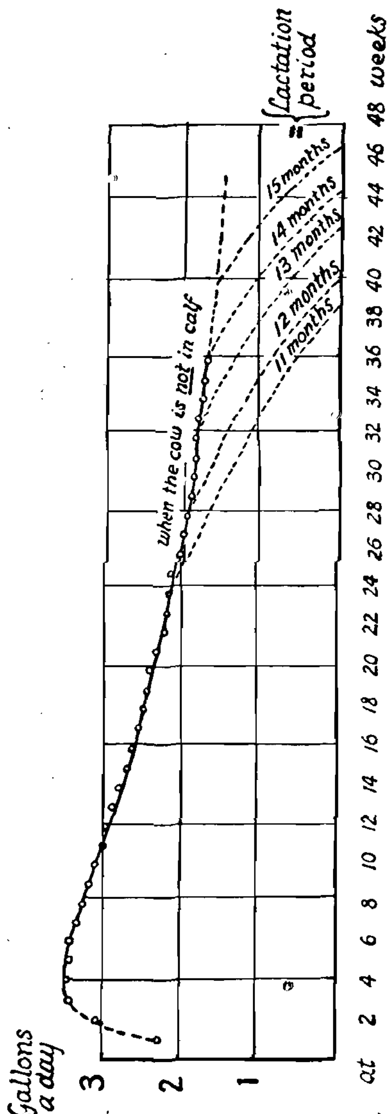
670 gallons, her yield as an eight-year-old will be 1000 gallons $\left(670 \times \frac{100}{67} = 1000\right)$. To say that her yield at two or three years old was 500 gallons does not mean that the cow was exactly two or three years old when the calf was born which started the yield, but, on the average, that her age was near 2½ or 3½ years.



If a cow's yield in a year be any number of gallons, her yield every day of the year is not that number divided by 365. If a yield be 730 gallons in a year, it is not 2 gallons every day. It may start at about 2 gallons a day, but, in three or four weeks, it will have risen to over 3½ gallons a day, then slowly declined to zero, a few weeks before next calving time. The diagram on p. 132 shows how the yield rises and falls during a lactation period. It is constructed from figures collected by Mr. W. Gavin in Lord Rayleigh's herds and from others collected from Ayrshire records. The long continuous line, which represents Mr. Gavin's figures, shows how the yield runs with cows which are not in calf again, the dotted falling lines how it runs with cows which are to calve again at from eleven to fifteen months after their previous calving. These falling lines are constructed from Mr. Gavin's observation that the cow's yield is not affected by her being in calf till she is within about twenty-four weeks of calving, and from Mr. Gavin's observations and others made on Ayrshire records to show how the yield is reduced when the lactation period is a month short, and how it is increased when the lactation period is from one to three months over the normal lactation period of twelve months. The average reduction for an eleven months' lactation is probably about 20 to 25 gallons, the average increases for thirteen, fourteen, and fifteen months' lactations are probably about 30, 60, and 90 gallons. But these figures are still tentative.

The chief deviations are caused by feeding, date of calving, the "condition" of the cow before calving, ill-health, housing, shelter, and rough and exciting treatment. The cow which yields 1000 gallons in one feeder's hands may give 25 per cent. more in another's, the cow which calves in autumn or winter and is house-fed may give 10 to 15 per cent. more than the cow calving in spring or summer, and the cow in good condition before calving much more than the cow in poor condition. The effects of the other causes of deviations can scarcely be estimated.

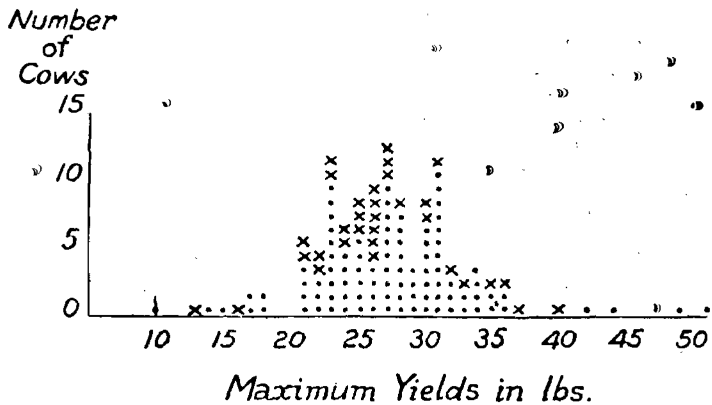
But, luckily, these deviations and their causes may be neglected, for, if she be in good health, the cow's yield,


Gallons a day
3
2
1
at 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42 44 46 48 weeks
Lactation period
when the cow is not in calf
15 months
14 months
13 months
12 months
11 months

at the flush, a few weeks after calving, is affected by none of them, and is a fair indication of what the normal yield is likely to be. This was found simultaneously by Mr. Gavin and the writer of this volume, who were working at the problem unknown to each other. If the yields at the flush be plotted on squared paper and a smoothed-out curve run through them, the normal lactation yield of a winter-calved cow is found by multiplying the daily yield at the top of the curve by 200. Mr. Gavin's plan is simpler, and needs no squared paper. He finds the daily yield at the flush, which he calls the "revised maximum," by taking the highest yield which is maintained over three successive weighings. If, for instance, a cow give 37, 38, 40, 39, and 37 pounds of milk at five successive weighings, the revised maximum is 38. Besides being a fair—probably the fairest—method of determining a cow's grade and finding her normal annual yield, this method has the important advantage of placing a cow in her grade shortly after calving.

Unfortunately, because it is desirable to have figures from a herd in which weekly records have been kept with great care for a considerable time from which the first lactation yields of the daughters of a fair number of bulls could be compared with those of their dams, also in their first lactations, our figures are not very many. Such as they are, however, we can speculate with them as we speculated with the Danish butter-fat figures.

The following diagram is constructed from the records of 128 first-calf Shorthorn heifers of similar type and weight belonging to four different herds: Captain T. A. Clarke's, at Farran, County Cork, and the Department of Agriculture's farms at Clonakilty, County Cork, Athenry, County Galway, and Ballyhaise, County Cavan. The diagram shows how many of these heifers gave one or another quantity of milk—from 10 to 50 pounds a day—at the flush, shortly after calving. The yields are reduced to what they should have been had every heifer been exactly three years old at calving. Captain Clarke's heifers are indicated by dots, the others by crosses.



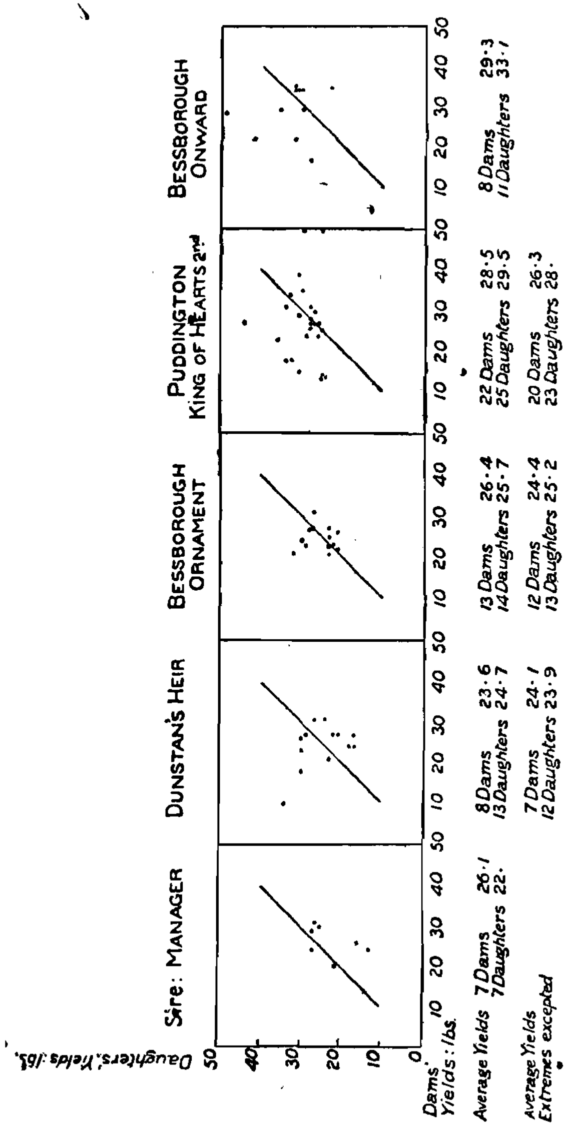
It will be noticed that, in the middle of this diagram, there are three peaks 3 or 4 pounds apart, indications of others not far away, and of others still as far away as 50 and 10 pounds. If these last two figures be the extremes and the intervening grades differ from each other by 3 or 4 pounds, then there must be twelve or thirteen grades, at least. And, if there are either of these numbers, there must be sixteen grades and four pairs of characters and factors. And the four highest factors, when carried together by the same animal, should produce about 50 pounds of milk, the four lowest about 10. Either the higher factor of a pair or the lower may be the dominant: but which need not be considered meantime. Let us assume that the higher factors are the dominants, and that the values of dominants and recessives are 20 and 4, 15 and 3, 10 and 2, and 5 and 1. By the ordinary chance distribution of these four pairs of factors, the following sixteen combinations and yields should be produced:

				Yield (Lbs.).
20	**15**	**10**	**5**	50
20	**15**	**10**	1	46
20	**15**	2	**5**	42
20	3	**10**	**5**	38
4	**15**	**10**	**5**	34
20	**15**	2	1	38
20	3	**10**	1	34
20	3	2	**5**	30
4	**15**	**10**	1	30
4	**15**	2	**5**	26
4	3	**10**	**5**	22
20	3	2	1	26
4	**15**	2	1	22
4	3	**10**	1	18
4	3	2	**5**	14
4	3	2	1	10

Of this speculation, as of the previous one, it may be said that it is not a very bad fit of the phenomena as these are at present known. And it may also help towards a better understanding of the problem. In this problem also, just as in that of butter fat, the production of a stock of animals breeding true to one grade or another is likely to be the first step towards accurate knowledge. In the meantime, no better method of raising the milk yield of a stock of animals can be suggested than that of using proved and tested sires and selecting young sires whose sisters are good yielders, that is from among the sons of already tested sires,[1] with, preferably, high-yielding dams. On this point the writer of this volume cannot do better than become personal. About fifteen years ago he was sent by the Irish Department of Agriculture to see and collect information from a few herds of dairy cattle in Ireland. In one herd he saw twelve or thirteen three-year-old heifers, all daughters of one sire, which were obviously unusually good milkers. The steward informed him, and the dairy-maid's records confirmed him, that the heifers' daily yields, at the flush, ran from 30 to 40 pounds a day. When asked to have the sire of the heifers brought out, the steward said that he had been sold to a new owner in England. Next morning the Irish Department telegraphed to the new owner to ask if he would sell the bull, and the same afternoon got the answer saying the bull "was sent to the butcher ten days ago." In another herd, half-a-dozen similar heifers, all daughters of one sire, were seen, and when a sight of the sire was asked for, the owner said, "Oh, he's in the Argentine."

The five following diagrams, which are constructed from the records of the daughters of five sires used in Captain T. A. Clarke's herd and their dams, will show that generally a milk sire may also be judged by his worst daughters as well as by his best. It will be seen that the yields run from 10 to 50 pounds, but that there are obvious grades near 16, 22, and 26.

[1] If some of the low-yielding factors are linked to the male sex, as Mr. Buchanan Smith has suggested, this direction may be wrong. In selection, the sire is less important than the dam.


Sire: Manager
Dunstan's Heir
Bessborough Ornament
Puddington King of Hearts 2nd
Bessborough Onward
Daughters' Yields: lbs.
Dams' Yields: lbs.
Average Yields 7 Dams 26·1 7 Daughters 22·
8 Dams 23·6 13 Daughters 24·7
13 Dams 26·4 14 Daughters 25·7
22 Dams 28·5 25 Daughters 29·5
8 Dams 29·3 11 Daughters 33·1
Average Yields Extremes excepted
7 Dams 24·1 12 Daughters 23·9
12 Dams 24·4 13 Daughters 25·2
20 Dams 26·3 23 Daughters 28·

XI

ECONOMIC AND GENERAL

A GENERALISATION like Mendel's attracts two different kinds of mind: the academic and the economic. The former seeks to develop and extend the generalisation, inquires into its foundations, and endeavours to discover not only the very nature of the "materials," but also the manner of their production and transmission. The latter is less interested in these "theoretical" or "scientific" problems, as he calls them, but accepts the generalisation with its formulæ and asks how they can be used towards an increased production of material wealth. That the Mendelian formulæ can be so used is now no longer in doubt. Pearl's and Nilsson-Ehle's results are proof sufficient. That the latter did not identify the actual factors for increased production and measure their individual effects may be a disappointment to the extreme "scientific" mind; but the economic mind is not to refuse Nilsson-Ehle's new varieties on that account. A new and effective febrifuge or an antiseptic which acts upon the internal tissues though applied on the skin are not to remain unused till the physiologist or the bacteriologist discovers how they do their work. If a stock of high-yielding dairy cattle is identified some day, their owners are not to delay breeding from them till the physiologist and the anatomist and the cytologist and the chemist have made a minute examination of their milk-producing machinery.

The possibilities of increasing the productivity of the vegetable world are enormous: be it in seeds and grains, roots and forage, stems and leaves, flowers, fibre, sugars and gums, tea, coffee, rubber, even timber. The initial step is to combine in one individual the factors already existing in two or more. These factors may be for quicker and stronger growth; for resistance to drought, frost, or disease; for greater activity in several directions, as in seed, or root, or leaf production, and so on. If the hybrid be a plant reproducible by buds, or shoots, or suckers, or in any other way than by seed, the new variety is already produced. Notable examples are the London plane, which now adorns the streets of many cities, the Huntingdon elm, the cricket-bat willow, the loganberry, the Up-to-Date and other varieties of potato.

The average yield of wheat in Britain is about 32 bushels to the acre. A rise of 25 per cent. would turn 32 bushels into 40. For every day by which the seed-time to harvest life of a variety of wheat is shortened, the northern wheat-growing limit in Canada is moved fifty or sixty miles nearer the North Pole. A vigorous, early ripening, and highly productive oat, and higher-yielding turnips and swedes, might improve the finances of many a northern or high-lying farm in Britain and even put many a pasture under the plough again, without the dangerous stimulus of a protective duty.

A century ago, Patrick Shirreff showed how new varieties, when found, can be tested, accumulated, and scattered broadcast. There have been other raisers of new varieties since Shirreff's time, but none whose work illustrates better what can and what cannot be done without Mendel's guide. For thirty years he persisted in hunting for new and better varieties in his own and his neighbours' fields, testing them, and accumulating stocks of the better ones. In this way he gave the country many new varieties. Then he began trying to get new varieties by cross-fertilisation, but lost himself among the many different varieties his crosses produced. He lived just a century too soon to succeed with cross-fertilisation.

In the beginning of the present century, Nilsson-Ehle with Mendel's work to guide him, saw that the second generation from the crossing parents, that is their hybrids' progeny, contains all the varieties likely to result from the cross, and that therefore the descendants of every second generation plant must be kept apart from all others as a single culture. Then the process of selection may begin: the most promising in yield and purity being retained, the others culled. The cultures retained are persistently "rogued" till the fifth generation: till later, if necessary: when the stock is usually large enough to be tested for yield. In a year or two, field trials are made, and the new variety approved or condemned.

Because of her success in breeding horses for speed, bullocks for beef, sheep for mutton, and pigs for pork and bacon, Great Britain has long been regarded as the greatest stock-breeding country in the world. But excepting for the race-horse, which has been selected and bred for three centuries chiefly upon the race-course test, these animals have been selected and bred for characters whose values were appraised by the eye and the hand, not by any method of exact or even approximate measuring or weighing. No one can say with certainty what difference a free use of the weighbridge would have made, but it may be suggested that bullocks which can produce 3 pounds of beef a day would now be more plentiful, and bullocks which can produce only 1½ or 2 pounds, fewer.

With animals whose fitness for their purpose can be tested only by careful weighing and measuring, Britain had no great success till a quarter of a century ago, when the late John Speir, a Lanarkshire farmer, who was familiar with what the Scandinavian farmers were doing to improve their milking cattle, induced the breeders of Ayrshire cattle to follow their example and measure their cows' yields systematically. The results were that, if the yields of the three-year-old heifers recorded in the years 1903 to 1907 be set down at 73, those recorded in 1908 and 1909 must be set down at 76, those in 1913 at 80, and those in 1920 at 84; that is, in fifteen years a rise of about 15 per cent. But, though the annual yield which leaves a profit to the farmer is seldom very far below 600 gallons, there are many cows in the country, even among Ayrshires, which yield considerably less. In some breeds, if not in most, there are cows whose milk contains over 5 per cent. of butter fat, but the average for the country is only about 3·7 per cent., and, even in the butter breeds, the milk of some cows contains no more butter fat than the general average. Thus, there is great need for more milk measuring, discarding unprofitable stock, and, above all, following the example set at Kolle Kolle by Mr. Grut Hansen.

If only a few millionaires would offer prizes to their nearest agricultural societies to be awarded for the best bull sent into the show ring followed by four or five of his daughters in milk, the tragedy of seeing so many sires sent to the butcher before their reproductive value had been proved might be averted.

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