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AN EXAMPLE OF THE MULTIPLE COUPLING
OF MENDELIAN FACTORS.

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[Authors alone are responsible for all opinions expressed in their Communications.]

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XXX.

AN EXAMPLE OF THE MULTIPLE COUPLING OF
MENDELIAN FACTORS.

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THE history of the English Campine varieties of fowl, as told in two pamphlets, "The Campine" and "The Production of the English Type Gold Campine," by the Rev. E. Lewis Jones, reveals the coupling of more than two factors in the presence of uncoupled factors having effects similar to those of the coupled factors.

Multiple coupling was revealed in the Cambridge experiments with sweet peas. Two varieties, *Duke of Westminster* and *Painted Lady*, whose flowers differed from each other in three pairs of characters, were mated, and, in the progeny of their hybrids there were only three groups instead of eight, as there should have been, had there been no coupling.

Multiple coupling is undoubtedly common, and is very obvious in regard to sex, since many characters invariably follow either the one sex or the other.

In the Campine fowl the factor for femaleness is coupled with two other factors at least; but, because of the presence of uncoupled factors having similar effects, the same sex is not always followed by the same characters.

A well known case of a similar nature, but in which only two factors are coupled, might be quoted by way of introduction.

It has already been shown that in fowl the males are pure as regards the factors for sex, while the females are hybrid. The two sexes may therefore be represented factorially as—

Male.	Female.
<i>M M</i>	<i>M F</i>

When pure barred males are mated with plain feathered females the progeny are all barred: from which it can be inferred that barring is dominant to plainness. On the other hand, when pure bred barred females are mated with plain males, only half the progeny are barred, while the other half are

plain. From this it can be inferred that barred females, though pure bred, according to the poultry breeders, are not genetically pure for barring, but carry a factor for plainness in addition. Pure bred barred fowl may therefore be represented as follows:—

Males.	Females.
$M M$	$M F$
$B B$	$B p$

Nor can the females be bred pure for barring: they carry always a factor for plainness. Males, however, can be bred pure either for barring or plainness. Thus the four following kinds of fowl may be represented factorially as follows:—

Barred males.	Barred females.	Plain males.	Plain females.
$M M$	$M F$	$M M$	$M F$
$B B$	$B p$	$p p$	$p p$

In addition to this there is the striking phenomenon that the barred progeny of barred females and plain males are all males, while the plain progeny are all females; and of this phenomenon the only possible explanation is that, while the factor M can associate with either B or p , F can associate with p only. The latter two are coupled together. Surrounding the factors F and p with a closed bracket, to prevent confusion, we may therefore represent the barred males and females factorially as—

Males.	Females.
$M M$	$M \begin{array}{ c } F \\ p \end{array}$
$B B$	$B \begin{array}{ c } p \end{array}$

The English Campines are descended from Belgian stock, the first of which were brought to England about a quarter of a century ago. The Belgian stock were of two kinds as regards colour: a silver and a gold, and both kinds were barred. But, while the hens were barred all over, excepting on the hackle, the cocks were unbarred not only on the hackle, but also on the back and tail. Occasionally cocks appeared as fully barred as the hens, but such were not preserved by the Belgian breeders. English breeders, on the other hand, preferred these fully barred males, and, preserving them, eventually produced silver and gold varieties of the breed which were equally fully barred in both sexes. The fully barred fowl are spoken of as of "English type," the others as of "Belgian type."

The fact that the Belgian hens are always of English type, while the cocks, which are usually Belgian, may be of English type occasionally, is clear evidence that the factor for English type is coupled with femaleness.

And the further fact that Belgian cocks have not the power of leaving all their progeny Belgian is also clear evidence that the English type is dominant to the Belgian.

Thus, putting E for English type and b for Belgian, the Belgian breed of fowl may be represented factorially so far as type is concerned, thus:—

Males.	Females.
$\begin{array}{cc} M & M \\ b & b \end{array}$	$\begin{array}{c} M \quad \boxed{F} \\ b \quad \boxed{E} \end{array}$

The male birds of English type which appear occasionally among Belgian stock may therefore be represented by $\frac{M}{b} \frac{M}{E}$, and the mothers of such birds

must have carried the factors $\frac{M}{E} \frac{F}{E}$.

That the silver colour is dominant to the gold and the factor for gold coupled with that for femaleness is brought out by several results mentioned in Mr. Jones's pamphlets; for, when silver males are mated with gold females the progeny are all silver, but when gold males are mated with silver females only half the progeny are silver, while the other half are gold. Besides, the silver progeny are all males, while the gold progeny are all females. The factor for gold colour is thus coupled with that for femaleness.

The factorial representation of the Belgian and English Campines becomes therefore:—

Belgian silver males.	Belgian silver females.	Belgian gold males.	Belgian gold females.	English silver males.	English silver females.	English gold males.	English gold females.
$\frac{M}{b} \frac{M}{S}$	$\frac{M}{b} \frac{\boxed{F}}{\boxed{E}} \frac{g}{g}$	$\frac{M}{b} \frac{M}{g}$	$\frac{M}{b} \frac{\boxed{F}}{\boxed{E}} \frac{g}{g}$	$\frac{M}{E} \frac{M}{S}$	$\frac{M}{E} \frac{\boxed{F}}{\boxed{E}} \frac{g}{g}$	$\frac{M}{E} \frac{M}{g}$	$\frac{M}{E} \frac{\boxed{F}}{\boxed{E}} \frac{g}{g}$

Although it is unnecessary, for the above hypothesis is clear as it stands, it might be well to show how it can be confirmed by a selection from Mr. Jones's experiments.

I.

English silver male.	and	Belgian gold female.	should give	English silver males.	and	English silver females.
$\frac{M}{E} \frac{M}{S}$		$\frac{M}{b} \frac{\boxed{F}}{\boxed{E}} \frac{g}{g}$		$\frac{M}{b} \frac{M}{S} \frac{g}{g}$		$\frac{M}{E} \frac{\boxed{F}}{\boxed{E}} \frac{g}{g}$

Mr. Jones got 6 English silver males and 6 English silver females

II.

Hybrid.

and

Hybrid.

$$\begin{array}{c} M M \\ b E \\ S g \end{array}$$

$$\begin{array}{c} M F \\ E E \\ S g \end{array}$$

should give

English silver males.				English silver females.	English gold females.	English silver females.	English gold females.
$\begin{array}{c} M M \\ E E \\ S S \end{array}$	$\begin{array}{c} M M \\ E E \\ S g \end{array}$	$\begin{array}{c} M M \\ b E \\ S S \end{array}$	$\begin{array}{c} M M \\ b E \\ S g \end{array}$	$\begin{array}{c} M F \\ E E \\ S g \end{array}$	$\begin{array}{c} M F \\ E E \\ g g \end{array}$	$\begin{array}{c} M F \\ b E \\ S g \end{array}$	$\begin{array}{c} M F \\ b E \\ g g \end{array}$

Mr. Jones got English silver males, English silver females, and English gold females; and he writes that "the proportion of silver to gold females was generally equal."

III.

Hybrid silver male.

and

English (apparently impure) gold female.

$$\begin{array}{c} M M \\ b E \\ S g \end{array}$$

$$\begin{array}{c} M F \\ b E \\ g g \end{array}$$

should give

English silver males.	English gold males.	Belgian silver males.	Belgian gold males.	English silver females.	English gold females.	English silver females.	English gold females.
$\begin{array}{c} M M \\ E b \\ S g \end{array}$	$\begin{array}{c} M M \\ E b \\ g g \end{array}$	$\begin{array}{c} M M \\ b b \\ S g \end{array}$	$\begin{array}{c} M M \\ b b \\ g g \end{array}$	$\begin{array}{c} M F \\ E E \\ S g \end{array}$	$\begin{array}{c} M F \\ E E \\ g g \end{array}$	$\begin{array}{c} M F \\ b E \\ S g \end{array}$	$\begin{array}{c} M F \\ b E \\ g g \end{array}$

Mr. Jones got English silver males, English gold males, Belgian silver males, Belgian gold males, and English silver females and English gold females. Mr. Jones cannot now give the proportions.

IV.

Hybrid silver male.	and	English (pure) silver female.
$M M$		$M \begin{bmatrix} F \\ E \\ S \end{bmatrix}$
$E b$		
$S g$		

should give

English silver males.				English silver females.	English gold females.	English silver females.	English gold females.
$M M$	$M M$	$M M$	$M M$	$M \begin{bmatrix} F \\ E \\ S \end{bmatrix}$	$M \begin{bmatrix} F \\ E \\ g \end{bmatrix}$	$M \begin{bmatrix} F \\ E \\ S \end{bmatrix}$	$M \begin{bmatrix} F \\ E \\ g \end{bmatrix}$
$E E$	$E E$	$E b$	$E b$	$E E$	$E E$	$b E$	$b E$
$S S$	$S g$	$S S$	$S g$	$S g$	$g g$	$S g$	$g g$

Mr. Jones got English silver males and females, and English gold females. He writes that this experiment was carried out by several people, and that taken altogether the proportions were 4 : 3 : 1. The proportion of silver to gold females should have been 1 : 1. The discrepancy is likely to be accounted for by some of the females not having been pure for English type. The English silver breed is only about ten years old, and undoubtedly many hens which breeders consider pure are not pure genetically.

It will be well to bring the foregoing result into line with previous work. Castle and Pearl showed that the American Barred Plymouth Rocks are merely black fowl having portions of their feathers lacking colour, i.e. barred. The "silver" Campine is therefore a black fowl with colourless bars on its plumage; and the black colour is dominant to the golden. Then, putting *Bl* for black and *Bd* for barred, a silver Campine hen of the Belgian breed is factorially represented by

$$\begin{matrix} M \\ b \\ Bl \\ Bd \end{matrix} \begin{bmatrix} F \\ E \\ g \\ p \end{bmatrix}$$

NOTE.—It will be noticed that experiments II and IV are apparently the same, but, in the former, the hens, though hybrids, were necessarily pure for *E*, while, in the latter, the hens were not necessarily pure for *E*, though "pure bred" from the breeder's standpoint.



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