

Rose comb: an example of operational over-dominance in the domestic fowl*

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(Received 21 December 1963)

Rose comb, a standard characteristic of several breeds and varieties of fowl, results from the action of a completely dominant autosomal gene, *R*. The recessive allele, *r*, gives rise to a single comb in birds homozygous for this allele. The inheritance of these comb types was first reported by Bateson (1902). Homozygotes (*RR*) and heterozygotes (*Rr*) are indistinguishable except by breeding tests, but both differ greatly from single comb (*rr*) individuals. The two phenotypes can be identified with ease, even in 15-day-old embryos.

Although Bateson's report was the first demonstrating that Mendel's laws applied to animals as well as to plants (Hutt, 1949), this knowledge has not been successfully utilized by poultry breeders. The Wyandotte breed provides a singular case of residual heterozygosity for a completely dominant gene and continues to produce single-comb segregates.

Hutt (1940) was the first to demonstrate conclusively that the reproductive ability of White Wyandottes was subnormal to that of some other breeds. He analysed records from official pedigree breeding stations in Lancashire and in Northern Ireland and showed that the number of chicks hatched per 100 eggs was consistently lower for White Wyandottes than for White Leghorns and Rhode Island Reds. Hutt attributed the subnormal reproduction to 'the pleiotropic action of some gene, or genes, determining the characteristics of White Wyandottes, or to linkage of deleterious genes with those making the breed.'

Cochez (1951) and Ponsignon (1951) found that reproductive performance of rose-comb birds was poorer than that of single-comb birds. Both investigators attributed this to a lethal factor linked to the gene for rose comb. Crawford & Merritt (1963) and Crawford & Smyth (1964*a*, 1964*b*, 1964*c*) conducted extensive studies of the reproductive efficiency of birds of the three comb genotypes (*RR*, *Rr*, *rr*) segregating in the Ottawa Meat Control Strain and in lines derived from this stock. A White Wyandotte strain was the original source of the rose-comb gene found in the Ottawa Meat Control Strain. The results relevant to the purpose of this discussion are as follows: (1) Low fertility was obtained from homozygous rose-comb males (*RR*) when mated either naturally or by artificial insemination.

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The heterozygous (Rr) and single-comb (rr) males contributed highly fertile matings. (2) There were no significant differences in fertility among females of the three comb genotypes regardless of the comb type of their mates.

An estimate of the effect of the homozygous rose-comb genotype on fertility and reproductive fitness is provided by results of natural matings of males of the three comb genotypes reported by Crawford & Smyth (1964*a*). Fertility determinations on a total of 2507 eggs provided the following percentages: homozygous rose-comb (RR) 77.9%, heterozygous rose-comb (Rr) 90.6% and single comb (rr) 91.8% fertile.

Thus, the gene for rose comb is pleiotropic in male fowls; and the effect of the gene on comb morphology is completely dominant, whereas the effect on fertility is recessive. These dual effects, when combined with the type of selection practised by poultry breeders attempting to eliminate the single comb gene (r), provide an interesting example of operational over-dominance.

Table 1. *Evaluation of the individual and combined pleiotropic effects of the gene for rose comb on reproductive rate and metric value*

Genotype	Reproductive rate	Metric value		
		Comb type ($s_R = 0; s_r = 1.0$)	Fertility* ($s_R = 0.07; s_r = 0$)	Index† ($s_R = 0.07; s_r = 1.0$)
RR	$1 - s_R$	1.00	0.93	0.93
Rr	1	1.00	1.00	1.00
rr	$1 - s_r$	0.0	1.00	0.00

* See text for basis of s_R .

† Combined fitness index of the effects of the rose-comb gene on fertility and constant artificial selection against the single-comb types.

An evaluation of the relative reproductive rates of (1) selection for rose comb by constant elimination of the single-comb types, (2) natural selection against the homozygous rose-comb genotype and (3) a fitness index combining the two criteria of selection are shown in Table 1. The notation of Wright (1931) is used where s_R = selection coefficient describing the reduction in the gametic contribution of the RR genotype and s_r = the comparable selection coefficient of the rr genotype. Over-dominance is indicated when both s_R and $s_r > 0$. The basis for the estimates of the reduction in the gametic contribution of the homozygous rose-comb individuals was the fertility data obtained from natural matings as reported above. The fertilities of eggs produced by matings of the rose-comb heterozygotes (90.6%) and single-comb birds (91.8%) were considered equal and assigned a value of 1.0. The 77.9% fertility of eggs produced from matings of homozygous rose-comb males is approximately 86% of the fertility of eggs obtained from matings of the other two genotypes. The 14% difference was divided by 2 to obtain $s_R = 0.07$

because the pleiotropic effect of the rose-comb gene on fertility is only expressed by males of the (*RR*) genotype. The precise value of s_R is not as important as the fact that it is greater than 0. It is probable that the magnitude of s_R would vary with strains and with environment as suggested by Munro (1946).

As both s_R and s_r are greater than 0, over-dominance for the combined index is clearly indicated. Wright (1931) has shown that the value of q at equilibrium can be estimated by the following formula:

$$q_R = \frac{s_r}{s_R + s_r} \tag{1}$$

where Wright's $s_A = s_R$ and $s_a = s_r$. Solving formula (1) for the conditions of the fitness index shown in Table 1, where $s_R = 0.07$ and $s_r = 1.0$, provides an estimate of the equilibrium frequency for the rose-comb gene of $q_R = 0.93$, and $1 - q_R = 0.07$.

Falconer (1960) in a discussion of over-dominance states: 'A pair of alleles with pleiotropic effects may be found not to exhibit over-dominance when any of the characters they affect are examined separately; yet if natural fitness or economic merit is founded on a combination of these characters, the alleles may show over-dominance with respect to fitness or merit.' Thus, the rose-comb gene as submitted to a combination of natural and artificial selection in the development of a rose-comb breed, the Wyandotte, provides an interesting example of over-dominance due to pleiotropy. This example has many similarities to the sort of over-dominance discussed by Falconer (1960) involving the pygmy gene in mice (King, 1955) and the sickle-cell anaemia gene (Allison, 1955).

The equilibrium frequency of $q_R = 0.93$ and $1 - q_R = 0.07$ provides an interesting explanation for the residual heterozygosity at the rose-comb locus in the Wyandotte. This breed of domestic fowl was admitted to the American Standard of Perfection in 1883. The rose-comb gene is a classical example of complete dominance and the approach to homozygosity without progeny testing would be admittedly very slow. However, the gene frequency for a gene of this type would be expected to be much higher than the estimated equilibrium frequency of $q_R = 0.93$ if selection against the homozygous single-comb genotype had been practised for 80 years and an estimated 60 or more generations. An estimated gene frequency can be obtained for the single-comb gene using the formula given by Falconer (1960).

$$q_t = \frac{q_0}{1 + t q_0} \tag{2}$$

where: t = number of generations of selection;

q_0 = original gene frequency of the single-comb gene (r);

q_t = gene frequency of the single-comb gene after t generations of selection.

Making the assumption that $q_0 = 0.5$ and $t = 60$ generations (assuming a generation interval of 1.3 years for an 80 year period and the conservative estimate that all birds of the original generation were heterozygotes, $q_R = 0.5$), solving formula (2) provides an estimate of $q_t = 0.016$. It should be noted that the choice of $q_0 = 0.5$

is quite arbitrary but that the value assumed for q_0 makes little difference to q_t . For example, if q_0 is assumed to be as high as 0.9 in formula (2), $q_t = 0.0164$. Thus, without considering the possibility that more effective selection methods, e.g. progeny testing, might have been used by certain poultry breeders, the estimated gene frequency for the single-comb gene would be approximately 20% of the equilibrium frequency expected with the degree of over-dominance shown in Table 1. Under the assumption of over-dominance, the expected segregation frequency of the single-comb type would be approximately 1 single-comb bird out of 200 individuals whereas under the assumption of no over-dominance, the expected frequency would be 1 single comb out of approximately 4000.

Observations on the segregation frequency of single-comb birds from White Wyandotte flocks were reported by Ponsignon (1951) as 14% of hatched chicks and by Cochez (1951) as 10 to 15%. Fredeen (1963) reported a segregation of 17% single-comb birds from a White Wyandotte flock maintained at the Experimental Farm, Lacombe, Alberta, Canada; and Gyles (1964) reported 17% single-comb segregants from a flock of White Wyandottes maintained at the University of Arkansas Experiment Station. These independent observations provide estimates of the gene frequency for the single-comb gene in White Wyandottes of 0.3–0.4 and support the hypothesis of operational over-dominance.

The estimated gene frequency of 0.3–0.4 for the single-comb gene is much higher than the estimated equilibrium frequency of 0.07 based on the reduced fertility of homozygous rose-comb males. The comparative fertility statistics used to estimate s_R were obtained from natural matings where the males of each genotype were not competing as they would be in flock matings involving both homozygous and heterozygous rose-comb individuals. For example, additional pleiotropic effects of the rose-comb gene are a reduced duration of fertility (Crawford & Smyth, 1964*b*) and a reduced copulation frequency (Crawford & Smyth, 1964*d*). However, the observation that homozygous rose-comb females lay fewer eggs as reported by Ponsignon (1951) has not been confirmed in these studies. If all of the additional pleiotropic effects of the rose-comb gene on reproductive fitness could be properly estimated, the equilibrium value for the rose-comb gene might well approximate the observed frequencies of this gene in flocks of Wyandottes.

SUMMARY

The pleiotropic effect of the rose-comb gene (R) on fertility when combined with artificial selection against the single-comb type (r) results in an interesting example of operational over-dominance. An evaluation of the equilibrium frequency of the rose-comb gene based on this over-dominance concept provides a plausible explanation for the relatively high frequency of single-comb birds appearing in the Wyandotte breed of fowls.

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