

# matters arising

## Assortative mating

VETTA<sup>1</sup> claims that Fisher's<sup>2</sup> well known formulae for the correlations between relatives under assortative mating are incorrect, and he presents alternative formulae for the parent-child and sib-sib correlations. I intend to publish elsewhere a simplified proof of Fisher's results, but it seems worthwhile to indicate here why I am not convinced by Vetta's argument.

Consider for simplicity the case in which there is no dominance and no environmental variability, so that all the variance is additive genetic. The alternative formulae for the parent-child correlation, which is in this case the same as the sib-sib correlation, are as follows

$$\begin{aligned} \text{Fisher: } & \frac{1}{2}(1+\mu), \text{ and} \\ \text{Vetta: } & \frac{1}{2}[1+\mu(1-\mu)^2] \end{aligned}$$

where  $\mu$  is the correlation between husband and wife. There is nothing in Fisher's model which restricts attention to positive, as opposed to negative, assortative mating, so that  $\mu$  may meaningfully take any value between  $-1$  and  $+1$ . Fisher's correlation increases linearly from  $0$  to  $1$  as  $\mu$  increases from  $-1$  to  $+1$ , which seems reasonable. Vetta's correlation is negative when  $\mu < -0.47$ , which seems implausible, and is less than  $-1$  when  $\mu < -0.87$ , which is impossible. Even if we confine our attention to positive values of  $\mu$  the behaviour of Vetta's correlation is strange, since it increases from  $0.5$  to  $0.574$  as  $\mu$  increases from  $0$  to  $\frac{1}{2}$ , and then decreases back to  $0.5$  as  $\mu$  increases further from  $\frac{1}{2}$  to  $1$ ; I find it difficult to understand how the correlation can fail to be an increasing function of  $\mu$ .

It is also quite easy to prove, at least to my satisfaction, that Fisher's correlation is correct in this case. Elementary genetic considerations show that the expected value for the child given full information about the complete genotypes of both parents is equal to the mid-parental value. Hence the regression of child on mid-parent is linear with unit slope, from which it follows that the parent-child correlation is  $\frac{1}{2}(1+\mu)$ .

Vetta claims that Fisher's formulae cannot be true in general because they predict that the parent-child correlation will in some circumstances exceed the sib-sib correlation; Vetta considers this to be impossible, but has given no reason to support this assertion.

I conclude that Vetta has failed to demonstrate that Fisher's formulae are incorrect, and that the alternative form-

ulae presented without proof in his paper are almost certainly incorrect.

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<sup>1</sup> Vetta, A. *Nature* 263, 316-317 (1976).

<sup>2</sup> Fisher, R. A. *Trans. R. Soc. Edinb.* 52, 399-433 (1918).

VETTA REPLIES—I consider<sup>1</sup> that the assumptions on which Fisher<sup>2</sup> derived his formulae are not valid for his model and Bulmer<sup>3</sup> raises no objection to this. His objections concern the parent-child correlations not being a linear function of  $\mu$ , the applicability of the model to disassortative mating and the excess of sib correlation over parent-child correlation. I consider these in turn.

Bulmer<sup>3</sup> claims that there is nothing in Fisher's model which restricts  $\mu$  and that it "may meaningfully take any value between  $-1$  and  $+1$ ". Unfortunately, the constraints of Fisher's model are not well understood. In fact,  $A$  ( $= \mu$  in Bulmer's example) cannot be increased to  $1$  without limit. For example, when  $A \approx 1$ , the increase in additive variance is infinitely large. It is difficult to conceive of any trait with infinite variance. That assortative mating could increase genetic variance to infinity is beyond belief. It is more likely that there are genetic constraints which ensure that the increase in variance brought about by a given degree of assortative mating will not be too large. The notion that  $A$  can be increased at will, to  $1$ , is unacceptable.

Is there any reason, apart from the formula  $\frac{1}{2}c_1c_2(1+\mu)$ , to assume that the parent-child correlation will increase linearly with  $\mu$ ? I know of none. Indeed, it is not absolutely clear how a non-linear increase,  $A\tau^2/(1-A)$  in the additive variance should give rise to a linear increase of exactly  $\frac{1}{2}A$  in the parent-child correlation. There is, therefore, no reason to believe that  $A$  can take any value between  $0$  and  $1$  and that the increase in the parent-child correlation should be exactly  $\frac{1}{2}A$ .

Are there any data which might indicate that an increase in  $\mu$  will, necessarily, result in an increase in the parent-child correlation? Data on human populations are scarce but studies<sup>4</sup> on racehorses, which have been bred assortatively for generations, do not support this assertion.

Fisher<sup>2</sup> showed that assortative mating (AM) will introduce association between phases of factors of an individual and this will increase the additive variance of the population. Wright<sup>5</sup> asserted that AM will also introduce correlation be-

tween the additive and dominance deviations of mates. I show that this, indeed, happens in Fisher's model. Fisher, however, did not take account of such correlations. In deriving my formulae, I take account of these and thus, provide a synthesis of Fisher and Wright on AM. I show that AM will (1) increase the association between additive deviations of a parent and his progeny and (2) introduce association between the additive deviations of one and the dominance deviations of the other. These considerations require a correction term to Fisher's formulae. This term, when  $c_1 = c_2 = 1$ , will be  $\frac{1}{2}A^2(A-2)$  for parent-child correlation. Note that when  $c_2 = 1, (2)$  is  $0$  but  $(1)$  is not  $0$ .

In Fisher's model  $A$  has two meanings: it is the genetic component of  $\mu$  and it also represents genetic correlation between phases of factors. It occurs in the former sense in Fisher's formulae and in the latter sense in my correction term. Obviously, when the correlation between phases of factors is  $0$ , that is, the population is mating assortatively for the first time, my correction term is  $0$ . I, therefore, assert that Fisher's formula for parent-child correlation, as given by Bulmer, is correct for a population which mates assortatively for the first time and is not correct for his model where the population is in equilibrium under a given degree of AM.

Geneticists<sup>6,7</sup> distinguish between assortative and disassortative mating because they have different genetical consequences. No polygenic model of disassortative mating is available. If one is constructed on the lines of Fisher's model, it will differ from the latter in three respects. First, there will be negative correlation between genotypes of an individual. Second, the genetic variance will decrease. And third, the correlation between the additive and dominance deviations of mates will be negative. Moreover, the attainment of equilibrium may present certain problems. Even if, for a given  $\mu$ , all these effects were exactly the same in the two models, the correlational formulae may still not be the same. Fisher<sup>2</sup> restricts himself to a model which results in "an increase in variance". Later<sup>8,9</sup> discussing it, he uses assortative mating and homogamy by which he means "the tendency of mating like with like" interchangeably.

I considered the possibility that, for his model, sib correction could be greater than the parent-child correlation but rejected it. Briefly, the reason is that, in presence of partial dominance, it is greater than parent-child correlation for one factor as well as for a large