# A correction to our earlier paper on 'The effect of repeated cycles of selection and regeneration in populations of finite size'

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Section 5 (Application of Method) of Curnow & Baker (1968) presents modifications to the recurrence equations when the sexes are differentiated. The modifications are not correct because they are based on the assumption that the expected genotypic frequencies at each generation are in Hardy-Weinberg equilibrium. If  $q_m$  and  $q_f$  are the male and female gene frequencies after a particular cycle of sampling and selection then the expected genotypic frequencies of the next generation following random mating will be

$$Q^2 - X$$
;  $2Q(1-Q) + 2X$  and  $(1-Q)^2 - X$ ,

where  $Q = \frac{1}{2}(q_m + q_f)$  and  $X = \frac{1}{4}(q_m - q_f)^2$  represent the average of the two gene frequencies and the deviation from Hardy-Weinberg equilibrium respectively.

Kojima's (1961) formulation, on which our paper was based, allows consideration of expected genotypic frequencies which are not in equilibrium. By following through his argument we find that

$$a\overline{k} (1-h) X$$

and

$$2a\overline{k} \ q \ (1-h) \ X + \frac{X}{2n_e} + \frac{aX\overline{k}}{2n_e} [(2-h)(1-2q) - (1-2h)(q^2 - X)]$$

should be averaged over the distribution of the gene frequency q and the disequilibrium X and then subtracted from our recurrence equations (6) and (7) respectively.

By deriving recurrence relations between the expected values of Q and X in one generation in terms of those in the previous generation, we can show that, with no selection,

$$E(X) = \frac{q(1-q)}{2(2n_e)^g(1+n_e^2)^{\frac{1}{2}}}[(n_e-1+\sqrt{(1+n_e^2)})^g-(n_e-1-\sqrt{(1+n_e^2)})^g],$$

where g is the number of cycles and q is now the initial gene frequency of the population before any sampling or selection has taken place.

Replacing X in the corrections above by its expected value assuming no selection should not lead to any great errors. This means that

$$a\overline{k} (1-h) E(X)$$

and 
$$E(X)\left[2a\overline{k}\;(1-h)\;\mu_1+\frac{1}{2n_e}\{1+a\overline{k}[(2-h)(1-2\mu_1)-(1-2h)(\mu_2-E(X))]\}\right]$$

need to be subtracted from the amended equations (6) and (7) in §5 of Curnow & Baker (1968). To take some account of selection the term q(1-q) in E(X) could be replaced by its current expected value  $(\mu_1 - \mu_2)$ .

Equations (10) and (11) for the probabilities of fixation also need to be amended. Equation (9) should, of course, have read

$$\mu_r = P_1 + \frac{(1 - P_0 - P_1) \mathcal{Q}(\mathcal{Q} + 1) \dots (\mathcal{Q} + r - 1)}{(\mathcal{Q} + m)(\mathcal{Q} + m + 1) \dots (\mathcal{Q} + m + r - 1)} \quad (r = 1, 2, 3, 4). \tag{9}$$

The amendments, correct to order E(X), are to subtract

$$\frac{(1-P_0-P_1)B(\cancel{\ell}+2n-2,m)}{B(\cancel{\ell},m)} nE(X)$$

$$\times \left[1 + \frac{ka[(1-2h)(\cancel{\ell}+2n-2)(nm-\cancel{\ell}-2n+1)+nm(\cancel{\ell}+2n+m-1)]}{(\cancel{\ell}+m+2n-1)(\cancel{\ell}+m+2n-2)}\right]$$

$$\times \left[1 + \frac{ka[(1-2h)(\cancel{k}+2n-2)(nl-m-2n+1)-nl(m+2n+\cancel{\ell}-1)]}{B(\cancel{\ell},m)}\right]$$

$$\times \left[1 + \frac{ka[(1-2h)(m+2n+\cancel{\ell}-2)(nl-m-2n+1)-nl(m+2n+\cancel{\ell}-1)]}{(\cancel{\ell}+m+2n-1)(\cancel{\ell}+m+2n-2)}\right]$$

from equations (10) and (11) respectively, where  $n = n_m + n_f$  and  $nk = n_m k_m + n_f k_f$ . It can be shown that the largest value of E(X), for  $n_e \ge 4$ , is 0.035 and so we are probably safe in ignoring the terms of order  $[E(X)]^2$ .

### SUMMARY

The basic recurrence equations given in our previous paper have to be modified when males and females are differentiated. The modifications we gave are incorrect because we ignored the deviations from Hardy-Weinberg equilibrium when sampling and selection are applied separately to the two sexes. Appropriate corrections are presented in this paper.

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### REFERENCES

Curnow, R. N. & Baker, L. H. (1968). The effect of repeated cycles of selection and regeneration in populations of finite size. *Genet. Res.* 11, 105-112.

Kojima, K. (1961). Effects of dominance and size of population on response to mass selection. Genet. Res. 2, 177–188.