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Why studies of the medionigra polymorphism in Panaxia dominula do not provide evidence for natural selection

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David Jones and Laurence Cook present a lengthy critique of recent papers by Denis F. Owen, Cyril A. Clarke and myself upon the *medionigra* polymorphism in *Panaxia dominula* L. Changes in phenotype frequencies in a population of *P. dominula* at Cothill, Oxfordshire, have been recorded for many years and interpreted as changes in allele frequency. We demonstrated that phenotype is determined at least in part by rearing temperature. The *medionigra* phenotype can be induced by either low or high temperatures in specimens from Cothill and from elsewhere (Owen and Goulson 1994, Goulson and Owen 1997). Thus changes in phenotype recorded in the wild cannot be directly translated into genotype frequencies. Jones and Cook argue at length that the *medionigra* phenotype is at least partially under genetic control, drawing evidence from a number of studies. I find their argument largely convincing, although evidence that the polymorphism is controlled by a single locus remains equivocal. Even casual inspection of either wild caught or captive bred *P. dominula* reveals that variation in the critical wing markings is continuous (Goulson and Owen 1997).

However, Jones and Cook have lost sight of a crucial point. The studies by E.B. Ford of the *medionigra* phenotype in *P. dominula* are primarily of significance for the role they played in the acrimonious Fisher–Wright debate on the relative importance of selection versus drift in determining genetic change. The interpretation of the Cothill data by E.B. Ford and R.A. Fisher was that changes in gene frequency were too great to be explained by stochastic processes, and therefore must be the result of selection (for example Ford 1964). Since very few other studies of gene frequencies in natural populations were available, these data became a central

plank in Fisher and Ford's argument. The crucial point is this: the statistics which demonstrate that changes in (presumed) allele frequencies were too great to be the result of drift depend on the ability of the researchers to precisely score gene frequencies. If the phenotype is determined in part by environmental effects, then their analysis becomes invalid. This is so even if there *is* a substantial genetic component.

Jones and Cook argue that since there is no clear relationship between mean June temperatures and phenotype frequencies, temperature cannot be important. They overlook the fact that *medionigra* phenotypes arise from either high or low temperatures (Owen and Goulson 1994), and that we have no idea of the timing or duration of the sensitive period(s) during development (Goulson and Owen 1997). It is thus naive to expect phenotype and temperature to be correlated in the ways they describe.

In summary, no convincing evidence has been presented that the *medionigra* polymorphism is controlled by a single locus. Even if crosses were carried out under controlled conditions, and offspring phenotype frequencies were in accordance with this hypothesis, we would still not know what proportion of *medionigra* phenotypes found in wild populations in any particular year were the result of temperature effects. The extensive data set on phenotype frequencies at Cothill cannot be used as evidence for natural selection.

Jones and Cook conclude by stating that it is a serious matter to allege that data have been distorted or suppressed. I agree entirely, but since I have never done so, I would like to add that it is an equally serious matter to mistakenly state that allegations of this sort have been made!

References

- Ford, E. B. 1964. Ecological genetics, 1st ed. – Methuen, London.
- Goulson, D. and Owen, D.F. 1997. Long-term studies of the *medionigra* polymorphism in the moth *Panaxia dominula*: a critique. – *Oikos* 80: 613–617.
- Owen, D. F. and Goulson, D. 1994. Effects of temperature on the expression of the *medionigra* phenotype of the moth *Panaxia dominula* (Lepidoptera: Arctiidae). – *Oikos* 71: 107–110.