

NOTES AND COMMENTS

THE EFFECTS OF SIMULTANEOUS DISRUPTIVE AND STABILISING SELECTION

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1. INTRODUCTION

DIRECTIONAL, stabilising and disruptive selection do not form mutually exclusive situations: in nature a character may be subjected to combinations of these forms of selection (Mather, 1943). For example, demonstration of the simultaneous action of directional and stabilising selection comes from the work of Karn and Penrose (1951), Kurten (1957) and Van Valen (1963). Simultaneous disruptive and stabilising selection involves selection against intermediate types, but simultaneously selection against the very extremes. The data of McNeilly (1968) and McNeilly and Bradshaw (1968) indicate that when copper tolerant populations on mines are subjected to gene flow from non-tolerant pasture populations, the progeny includes genotypes which are more tolerant than any adults found on the mine. Over-tolerant genotypes appear to be at a disadvantage (see Antonovics, Bradshaw, and Turner, 1971, for full discussion). Although in these examples there is no stabilising component with regard to selection against tolerance on the pasture (*i.e.* extremely non-tolerant individuals are not selected against), it is possible to envisage that such a situation might occur between two niches that are both toxic but which differ in their degree of toxicity.

During a simulation of sympatric divergence in a two-niche environment (for full description see Dickinson and Antonovics, 1972) a model of mixed disruptive and stabilising selection was investigated to study the effect of this type of selection on the genetic structure of the population.

2. THE MODEL

The model was the same as the two-gene model described by Dickinson and Antonovics (1972) except in the pattern of the selection pressures. The assumptions were as follows. There were two niches, X and Y, with interbreeding populations. The size of the population in each niche remained constant and generations were separate. There was gene flow between the two niches and it remained at the same level in successive generations. Only males migrated; mating occurred after migration and the offspring were subjected to selection in the environment where they were produced. Genes *A/a* and *B/b* controlled a character which was such that

alleles *A* and *B* were favoured in niche X and, conversely, alleles *a* and *b* were favoured in niche Y. The genotypes had the fitness shown below:

		<i>AAbb</i>	<i>Aabb</i>	<i>aaBB</i>	<i>aabb</i>
	<i>AABB</i>	<i>AaBB</i>	<i>AaBb</i>	<i>Aabb</i>	<i>aabb</i>
(a) Simultaneous stabilising and disruptive selection:					
Niche X	$1-s$	$1-\frac{1}{4}s$	$1-\frac{1}{2}s$	$1-\frac{3}{4}s$	$1-s$
Niche Y	$1-s$	$1-\frac{3}{4}s$	$1-\frac{1}{2}s$	$1-\frac{1}{4}s$	$1-s$
(b) Disruptive selection alone:					
Niche X	1	$1-\frac{1}{4}s$	$1-\frac{1}{2}s$	$1-\frac{3}{4}s$	$1-s$
Niche Y	$1-s$	$1-\frac{3}{4}s$	$1-\frac{1}{2}s$	$1-\frac{1}{4}s$	1

3. RESULTS AND DISCUSSION

As expected, a combination of disruptive and stabilising selection resulted in a lower mean divergence between the sub-populations, a lower overall population variance and a slightly lower variance within sub-populations than when stabilising selection was absent. When stabilising selection was acting, the overall variance decreased as the selection pressure increased, whereas in the absence of stabilising selection the converse was true. The inclusion of stabilising selection caused the overall variance to be lower after selection than before selection and again, the converse held for disruptive selection alone.

Mixed stabilising and disruptive selection resulted, in both niches, in an appreciable excess of heterozygotes over that predicted by the Hardy-Weinberg law, particularly under intense selection. The absolute number of single and double heterozygotes was greater under mixed selection than when there was disruptive selection alone. Stabilising selection also ensured that a polymorphism could be maintained over a much wider range of conditions of asymmetric gene flow and selection. This pattern of selection may therefore be another contributory explanation for the high level of heterozygosity and polymorphism found in natural populations.

In addition to the effects of heterozygosity, mixed stabilising selection resulted in negligible zygotic association (Allard, Jain and Workman, 1968), whereas under disruptive selection there were extremely high levels of zygotic association. This quantity is positive if there is an excess of double homozygotes and double heterozygotes over those obtaining from random assortment and negative if the converse is true. Therefore, zygotic association, which may be expected as confirmatory evidence of a simple disruptive selection situation, would not be detected in a population subjected to mixed selection.

These results further emphasise the difficulties in attempting to deduce the forces acting on a population from field observations. Even if the level of gene flow is known, the same level of any single population parameter may result either from a particular intensity of disruptive selection or from a quite different intensity of mixed selection. In a particular niche, changes in variance of a character over age classes or with time would not reveal the action of both stabilising and disruptive selection. For this to be detected the selection acting on each phenotypic class needs to be known (cf. Slatkin, 1970).

The model presented here illustrates the additional complexities that result when natural patterns of selection are imposed on idealised models and provides a further mechanism for maintaining high levels of heterozygosity in natural populations.

4. REFERENCES

- ALLARD, R. W., JAIN, S. K., AND WORKMAN, P. L. 1968. The genetics of inbreeding populations. *Adv. Genet.*, *14*, 55-131.
- ANTONOVICS, J., BRADSHAW, A. D., AND TURNER, R. G. 1971. Heavy metal tolerance in plants. *Advances in Ecological Research*, *7*, 1-85.
- DICKINSON, H., AND ANTONOVICS, J. 1972. Theoretical considerations of sympatric divergence. *Am. Nat.* (in press).
- KARN, M. N., AND PENROSE, L. S. 1951. Birth weight and gestation time in relation to maternal age, parity, and infant survival. *Ann. Eugenics*, *161*, 147-164.
- KURTEN, B. 1957. A case of Darwinian selection in bears. *Evolution*, *11*, 412-416.
- MATHER, K. 1943. Polygenic inheritance and natural selection. *Biol. Rev.*, *18*, 32-64.
- MCNEILLY, T. 1968. Evolution in closely adjacent plant populations. III. *Agrostis tenuis* on a small copper mine. *Heredity*, *23*, 99-108.
- MCNEILLY, T., AND BRADSHAW, A. D. 1968. Evolutionary processes in populations of copper tolerant *Agrostis tenuis* Sibth. *Evolution*, *22*, 108-118.
- SLATKIN, M. 1970. Selection and polygenic characters. *Proc. Natn. Acad. Sci., U.S.A.*, *66*, 87-93.
- VAN VALEN, L. 1963. Selection in natural populations: *Merychippus primus*, a fossil horse. *Nature*, *197*, 1181-1183.

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