

NATURAL SELECTION ON THE POLYMORPHIC SNAIL
HYGROMIA STRIOLATA

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SUMMARY

Hygromia striolata (C. Pfeiffer) is polymorphic for shell and mantle colour. Thirty-two samples were taken from natural populations in the region of Malham, Yorkshire. The samples were taken in pairs, one member of each pair from a habitat with a relatively dark background and one from a nearby habitat with a relatively light background. In general, samples from "darker" habitats had higher proportions of the dark-shelled and dark-bodied morphs. These associations are highly significant, and they can most easily be explained in terms of visual selection by predators.

1. INTRODUCTION

LAND molluscs have a number of advantages (such as low mobility, high abundance and a wide range of ecological tolerance) that make them very suitable for research on the genetics of natural populations. A disproportionate amount of this research has been carried out on the common British snails *Cepaea nemoralis* and *C. hortensis*. These species possess a complex and easily scored system of genetic variation in shell colour and banding, whose mode of inheritance is well understood (Cain, Sheppard and King, 1968). There are remarkable patterns of local change in the frequencies of the polymorphic genes (for recent review, see Jones, 1973). It is possible to associate some of these patterns with environmental factors. The best-known example of such an association is found in populations of *C. nemoralis* from contrasting habitats in lowland southern England (Cain and Sheppard, 1954). Woodland populations have a relatively high frequency of unbanded pink and brown shells, which harmonise with the background of leaf litter, while populations from open habitats (such as grassland) have a relatively high frequency of banded yellow shells. The association is apparently due to natural selection by thrushes and other predators, which take an unduly large proportion of the more conspicuous morphs in each habitat (Sheppard, 1951). *C. hortensis* utilises a different series of genes to attain a visually similar result (Clarke, 1962), while the related Helicid *Arianta arbustorum* also shows an association of morph frequency with background (Parkin, 1971), although this species is much less polymorphic than *C. nemoralis* or *C. hortensis*.

The present paper reports associations with background vegetation among populations of *Hygromia striolata* (C. Pfeiffer) in the vicinity of Malham, Yorkshire.

2. VARIATION IN *H. striolata* IN THE MALHAM AREA

H. striolata is much smaller than *Cepaea* or *Arianta*, and has a less clear-cut polymorphism (Cain, 1959a). The shell may be heavily pigmented and dark reddish-brown (var. *rubens* of Taylor, 1916), or unpigmented and a light fawn colour. The mantle may be black or light-coloured. As the shell is translucent, it is often possible to see the colour of the mantle through the shell. Variations in mantle colour are known to be inherited (Cain, 1959b). In the Malham area *H. striolata* is common in a variety of habitats, including short grass on scree slopes, hedgerows and mixed deciduous woods (Cameron and Redfern, 1972). During 1965 and 1966 we collected 16 pairs of samples. The members of each pair were taken from contrasting habitats, as close to each other as possible (the distances between them vary between 5 m and 700 m). Snails were scored for shell and mantle colour, and the

TABLE 1
Composition of samples of H. striolata from the Malham area

Grid ref.*	Total	Composition of samples				% Dark body	% Dark shell	Habitat	Background
		Dark body, dark shell	Dark body, light shell	Light body, dark shell	Light body, light shell				
1. 836663	54	3	37	0	14	74.1	5.6	N	Darker
836663	10	0	0	0	10	0.0	0.0	SG	Lighter
2. 838646	40	0	27	0	13	67.5	0.0	RH	Darker
837651	11	0	0	0	11	0.0	0.0	LG	Lighter
3. 890609	43	11	20	1	11	72.1	27.9	RH	Darker
890609	19	1	5	4	9	31.6	26.3	LG	Lighter
4. 891609	37	17	3	10	7	54.1	73.0	MW	Darker
894611	31	0	23	0	8	74.2	0.0	RH	Lighter
5. 892609	48	20	17	4	7	77.1	50.0	MW	Darker
892610	8	1	4	0	3	62.5	12.5	RH	Lighter
6. 895673	39	3	14	0	22	43.6	7.7	MW	Darker
896673	22	0	8	0	14	36.4	0.0	RH	Lighter
7. 898641	29	8	17	0	4	86.2	27.6	MW	Darker
898641	210	9	81	2	118	42.9	5.2	N	Lighter
8. 899706	48	7	35	0	6	87.5	14.6	N	Darker
898708	29	4	16	0	9	69.0	13.8	SG	Lighter
9. 903606	60	16	26	3	15	70.0	31.7	MW	Darker
900612	65	4	34	6	21	58.5	15.4	RH	Lighter
10. 906649	6	3	1	0	2	66.7	50.0	N	Darker
912649	159	1	33	0	125	21.4	0.6	SG	Lighter
11. 909632	59	0	15	0	44	25.4	0.0	MW	Darker
911632	31	0	11	0	20	35.5	0.0	LG	Lighter
12. 917723	52	16	5	0	31	40.4	30.8	MW	Darker
924718	14	0	0	0	14	0.0	0.0	LG	Lighter
13. 981650	14	6	4	2	2	71.4	57.1	MW	Darker
979652	25	5	5	0	15	40.0	20.0	LG	Lighter
14. 985646	13	3	5	2	3	61.5	38.5	MW	Darker
985645	76	3	7	5	61	13.2	10.5	LG	Lighter
15. 988650	23	8	2	0	13	43.5	34.8	MW	Darker
989648	61	7	7	0	47	22.9	11.5	SG, N	Lighter
16. 983657	31	5	1	1	24	19.4	19.4	MW	Darker
982657	69	14	9	0	46	33.3	20.3	SG, N	Lighter

N = Nettles; SG = short grass; RH = rough herbage; LG = long grass; MW = mixed woodlands.
* All in grid square ND.

habitat of each sample was assigned to a “darker” or “lighter” class relative to the other member of the pair. Sample scores and habitat types are given in table 1.

There is a clear association between the frequencies of the polymorphic variants and background vegetation (fig. 1). Populations from “dark” habitats usually have higher frequencies of the dark shell and dark mantle morphs than do adjacent populations from light habitats. These associations are statistically significant.

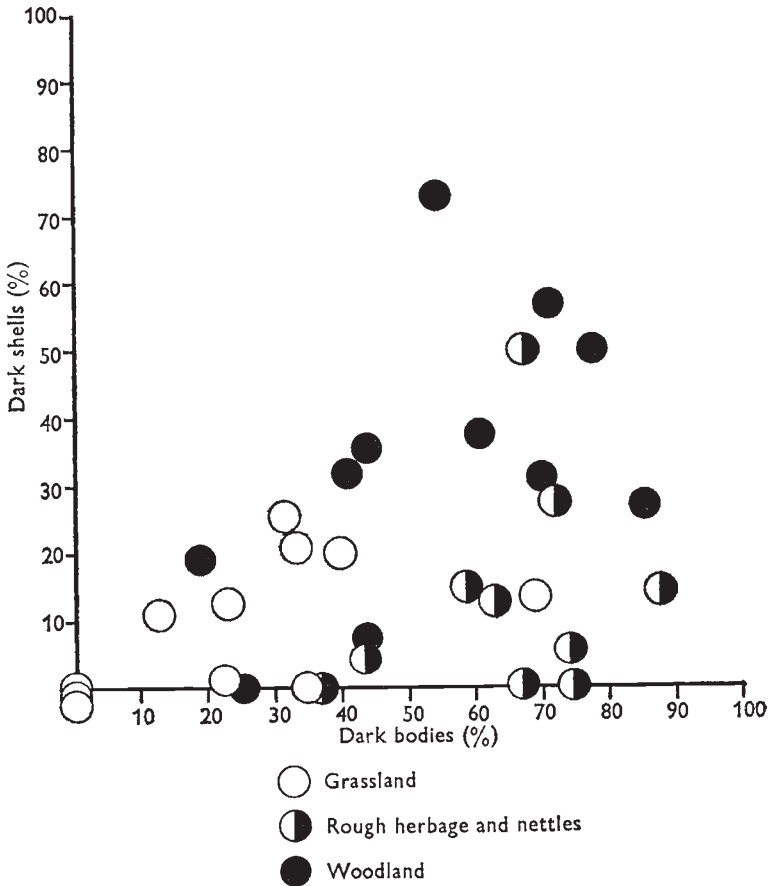


FIG. 1.—Association between morph frequency and background vegetation in populations of *Hygromia striolata* in the Malham area.

In 13 of the 16 pairs, the “darker” habitat had a higher proportion of dark shells, and in 3 it had a lower proportion. This discrepancy itself is significant ($P < 0.02$, by the median test). When the sizes of the individual differences are taken into account, using Haldane’s method of summing chi (Quenouille, 1950), the significance level becomes extreme

$$\frac{((\sum\chi)^2}{n} = 54.9, P < 10^{-10}).$$

Similarly, in 13 of the 14 pairs that included dark-bodied shells, the "darker" habitat had a higher proportion of these variants, and in one it had a lower proportion ($P < 0.01$, by the median test; $P < 10^{-10}$, by Haldene's method).

3. DISCUSSION

The pattern of association of morph frequency with background vegetation in *Hygromia striolata* in the Malham area is parallel to that found in *Cepaea nemoralis* and *C. hortensis* in southern England, and is probably due to a similar visual selection by predators. *H. striolata* is frequently eaten by thrushes, and broken shells of this species are common around thrush anvils (Taylor, 1916; our own observations). Snails with dark shells and mantles are apparently more cryptic against the darker vegetational backgrounds, while those with light-coloured shells and mantles seem to be better concealed in the more light-coloured open habitats.

Unfortunately, neither in *Cepaea* nor in *Hygromia* is there any direct evidence of what factors act to maintain the polymorphism in the face of directional selection by predators. This selection might be expected to lead to uniform populations in each habitat, with each snail matching its background. Possible balancing mechanisms include a selective advantage of the heterozygotes over both homozygotes at each locus (as postulated for *Cepaea* by Cain and Currey, 1963) and frequency-dependent selection by predators acting to favour the rarer morphs (Clarke, 1962). Among *H. striolata* in the Malham area, populations from contrasting habitats are often very close together. Some of our pairs contain genetically distinct samples that are only 5 metres apart. Selection by predators favouring different genes in different vegetational backgrounds, with migration of snails causing gene flows between habitats, may therefore help to maintain a low frequency of the visually inappropriate morphs within each habitat.

There is some evidence of a "regional" influence on phenotype frequencies, in addition to the effects of visual selection. The frequency of dark shells is considerably lower (for both light and dark habitats) in the area bounded by Malham Tarn, Settle and Malham village than in the area south of Malham village and around Grassington and Arncliffe. Nonetheless, local associations of morph frequency with background occur in the whole study area. This pattern may be analogous to the "area effects" found in some populations of *Cepaea* (Cain and Currey, 1963), in which large ecologically diverse areas are characterised by a limited range of morph frequencies, while adjacent and apparently similar areas have quite different frequencies. Area effects in *Cepaea* are often maintained in the face of intense selective predation. The geographical differentiation in *H. striolata* is worthy of further investigation.

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THE EFFECT OF ENVIRONMENT ON HERITABILITY AND PREDICTED SELECTION RESPONSE: A REPLY

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DADAY *et al.* (1973) examined the possibilities of selection for the genetic improvement of some economic characters of *Medicago sativa* (L) in different environments, with a view to applying Hammond's ideas that a character will be most easily advanced by selective breeding in the environment in which it is most fully expressed.

Hammond's idea applies to two sets of conditions. When a genotype is too weak to express itself in the environment in which it is to be used, but will do so if the frequency of relevant alleles is increased, selection for the character concerned in circumstances in which the genotype is expressed will increase gene frequencies to the point where the genes are expressed in the original environment also. This is essentially the finding of Waddington's (1952) experiment with crossvein-less in *Drosophila melanogaster*. There have been numerous examples published since. A convenient illustration is the selection for the ability of rabbits to acquire immunity to myxoma virus. Unselected populations of rabbits exposed to virulent strains of virus suffered such a high mortality that virtually all infected rabbits died and hence there was no selection in favour of the better genotypes. However, when populations are exposed to strains with a case mortality of 90 per cent or less, survival of the better genotypes rapidly gives rise to populations in which there is some survival of individuals even after exposure to the more virulent strains (Sobey, 1969). Genetic variation, which is latent in one régime, is exposed and used by selection in a second, until eventually the genotype achieves expression in the first.