THE RELATION OF PHENOTYPE TO HABITAT IN AN INTRODUCED COLONY OF *CEPAEA NEMORALIS*

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Received 5.viii.74

SUMMARY

The introduced colony of *Cepaea nemoralis* at Lynchburg, Virginia, contains only yellow shells. The populations respond to the characteristics of the environment by adjusting the frequencies of the banding morphs and by regulating the amount of fusion of adjacent bands. In this respect they fulfill a prediction based on the observations of Clarke (1960) on British colonies of *Cepaea hortensis*.

In a classic study of polymorphism in the land snail *Cepaea nemoralis*, Cain and Sheppard (1950, 1954) have demonstrated the role of visual selection in determining the frequencies of the colour and banding morphs. Near Oxford, England, high frequencies of pink and brown unbanded shells are characteristic of dark woodland sites; yellow unbanded shells, of open grassy areas; and yellow bandeds, of hedgerows and mixed rough herbage. Subsequent work has confirmed these findings (Currey, Arnold and Carter, 1964), although not all areas show the effects of visual selection (Cain and Currey, 1963, 1968).

Lamotte (1959) has argued that if visual selection is an important determinant of morph frequency in these snails, then in mixed colonies of *C. nemoralis* and the closely related *C. hortensis* similar frequencies should occur in the two species. No such correspondence is found. Clarke (1960) has shown, however, that *C. hortensis*, a species in which the pink and brown morphs are rare, nevertheless responds to visual selection within the context of its own genetic system. In response to a dark background *C. hortensis* develops dark morphs by the fusion of the black bands of yellow, banded shells. Populations of *Cepaea nemoralis* in Lynchburg, Virginia, where only yellow shells are found, provide a unique opportunity to demonstrate a similar phenomenon in this species in the absence of pink and brown morphs.

Cepaea nemoralis was introduced into North America during the nineteenth century (Howe, 1898). The species was first reported in Lynchburg by Ortmann in 1926, the founders in all probability having been brought from the Lexington, Virginia, colony (Howe, 1898; Ortmann, 1926). Samples were taken by one of us (A. V. R.) from populations within the city in the springs of 1970 and 1971. Sampling areas were restricted to 100 square feet with homogeneous vegetation and exposure. All sites were searched carefully to avoid collecting higher frequencies of the more conspicuous morphs. Successive samples from the same locality showed no significant heterogeneity.

Shells were scored for age, condition and banding pattern according to the conventions of Cain and Sheppard (1954) and of Clarke (1960). Three primary categories are reported here: 00000 (unbanded only), 00300 (mid-banded, but including shells with faint traces of bands 4 and 5), and $\pm$ 12345 (containing all other banding types). Shells are separately classified as

" effectively unbanded " if they lack bands 1 and 2. The frequency of shells with fused bands is calculated as a proportion of the banded class, exclusive of effectively unbanded shells. Sampling areas were classified both according to type of vegetation and amount of shade. Scores for the Lynchburg samples are given in table 1. The data are reported in full elsewhere (Richards, 1972).

TABLE 1

The principal phenotypes in samples of Cepaea nemoralis *from Lynchburg, Virginia. Vegetational types: CG—Candytuft* (Iberis sempervirens) *and grass; HS—Honeysuckle* (Lonicera japonica)*; HR—Hedgerows of Privet* (Ligustrum *sp.*) *or Winter Jasmine* (Jasminum nudiflorum)*; I—Ivy* (Hedera *sp.*). *Sunlight: S—sunny; MS—mostly sunny; PSh—partly shaded; Sh—shady. 00300 includes shells with faint traces of bands 4 and 5; ±12345 includes all other types of bands. E.U. (effectively unbanded) includes all shells with bands 1 and 2 missing. Fusions are calculated as a proportion of the banded class, exclusive of effectively unbanded shells.*

			Percentage of adult phenotypes					
Locality	Vegetation	Sunlight	00000	00300	±12345	E.U.	Fusions	N
Breckenridge and Baltimore	HS	PSh	0·67	2·01	97·32	2·68	32·41	162
1100 Cabell	CG	PSh	47·62	0	52·38	47·62	21·21	63
2109 Cedar	CG	S	14·47	0	85·53	17·61	16·03	159
916 Commerce	HS	Sh	3·50	0	96·50	3·50	63·77	143
616 Court	HS	Sh	22·69	7·56	69·75	30·25	44·58	119
914 Federal	I	Sh	7·55	13·21	79·24	24·53	50·00	53
1319 Filmore	HS	S	0	0	100·00	1·02	9·28	98
1514 Fourteenth	CG	Sh	40·48	0	59·52	40·48	12·00	126
G. E. Center	HS	PSh	21·35	1·12	77·53	28·09	28·12	89
G. E. Side	CG	MS	31·71	0	68·29	32·52	13·25	123
301 Grayson	CG	PSh	9·52	0	90·48	11·90	27·03	42
Green and Otey Fence	HS	PSh	1·45	1·45	97·10	2·90	14·92	69
Green and Otey Wall	HS	MS	0	0	100·00	0·74	12·12	133
407 Langhorne	HR	PSh	4·90	4·90	90·20	12·75	19·10	102
409 Langhorne	CG	MS	23·70	0	76·30	28·92	9·60	249
822 Rivermont	CG	PSh	25·60	15·20	59·20	41·60	23·29	125
1306 Rivermont	CG	PSh	23·29	0	76·71	26·03	31·48	73
1382 Rivermont	HR	S	0	0	100·00	0	30·86	81
1607 Rivermont	CG	MS	28·73	21·84	49·43	50·57	13·95	87
2024 Rivermont	I	MS	9·72	0	90·28	9·72	13·85	72
Unitarian Church	I	Sh	28·20	5·13	66·67	33·33	34·62	39
106 Westover	HR	Sh	0	0	100·00	0	39·53	43
405 Westover	CG	MS	24·43	0	75·57	27·43	2·02	131
3406 Wilson	HS	MS	9·62	1·92	88·46	11·54	1·09	104
4818 Windsor	HS	MS	4·55	5·68	89·77	12·50	3·90	88
Yeardley and Sussex	HS	MS	3·57	1·79	94·64	5·36	11·32	56

The relationship between phenotype frequencies and background vegetation is shown in fig. 1, in which the proportion of unbanded shells in each sample is plotted against the proportion of fusions in the banded shells. These are the variables used by Clarke (1960) to demonstrate the correspondence of colonies of *C. hortensis* to differing habitats. A similar phenomenon is apparent from fig. 1. The candytuft/grass habitats have high frequencies of unbanded shells and few fusions among the bandeds. Honeysuckle sites have high frequencies of bandeds, usually with few fusions, although there

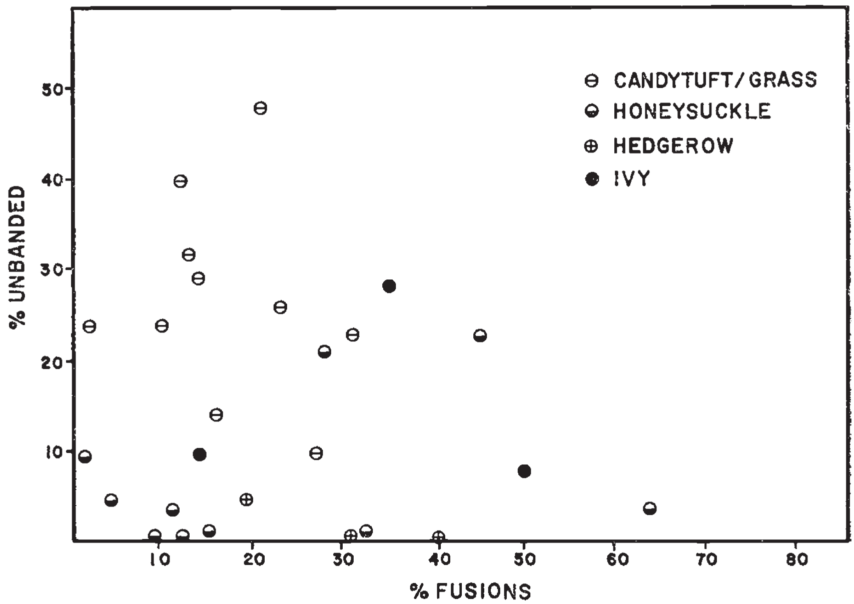

Fig. 1.—The relationship between morph frequencies and vegetation in samples of *Cepaea nemoralis* from Lynchburg, Virginia. The frequency of fusions is calculated as a proportion of the banded class, exclusive of shells with bands 1 and 2 absent.

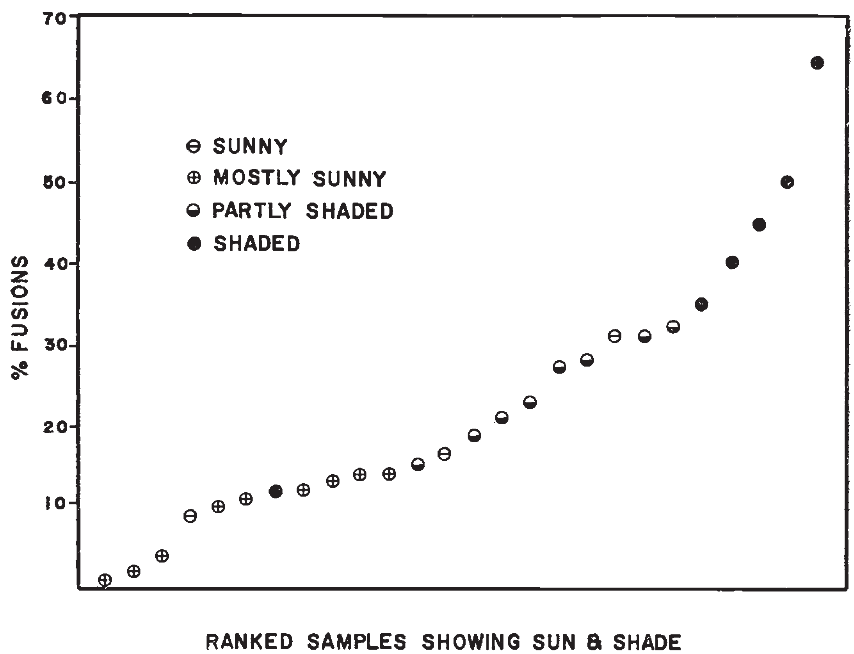

Fig. 2.—Samples of *Cepaea nemoralis* from Lynchburg, Virginia, ranked according to the frequency of shells with fused bands. High frequencies of fused bands are associated with shaded habitats.

are some notable exceptions (see below). Hedgerows are characterised by banded shells with high proportions of fusions. Analysis of variance indicates that the differences between vegetational categories are significant with respect to the proportion of unbanded shells ($F = 11{\cdot}19$; $P < 0{\cdot}001$).

The effect of vegetation on the proportion of fusion appears to be less important than the amount of sunlight falling on the site. Figure 2 shows the colonies ranked according to the proportions of fusions in each and indicates the relative exposure to sunlight. Shadier, and therefore darker, habitats have higher proportions of fusions than sunnier ones. Analysis of variance confirms this relationship ($F = 12{\cdot}18$; $P < 0{\cdot}001$).

Since associations of this sort could result fortuitously from the spatial grouping of similar habitats, a search was made for geographical associations among samples with similar phenotypic frequencies. No relationship could be found between the relative position of populations and their respective frequencies (Richards, 1972).

These results therefore fulfil the expectation based on Clarke's (1960) studies of *C. hortensis*. In the absence of pink and brown morphs, populations of *C. nemoralis* from Lynchburg, Virginia, respond to the characteristics of their environments by adjusting the frequencies of the unbanded and banded morphs and by regulating the degree to which adjacent bands are fused to produce a relatively uniform dark coloration.

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