DIVERGENT EFFECTS OF NATURAL SELECTION ON TWO CLOSELY-RELATED POLYMORPHIC SNAILS

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1. INTRODUCTION

THE shells of land snails of the genus *Cepaea* Held. display striking colour and banding polymorphisms which have attracted the attention of many workers, particularly as supposed examples of random variation. Cain and Sheppard (1954) have shown, however, that the proportions of different varieties in colonies of *Cepaea nemoralis* L. can be related to the colour and uniformity of the background. They explain this relation, but not the maintenance of the polymorphism itself, in terms of selective visual predation, which has been demonstrated by Sheppard (1951).

Lamotte (1951) admits the existence of visual selection, but regards it as unimportant. The most cogent of his arguments is that he can find no correlation between the variations in *C. nemoralis* L. and *C. hortensis* Müll. living together in mixed colonies. The two species are almost identical in appearance, show a similar range of phenotypes, and seem to share the same predators. Lamotte reasons that if visual predation were important in determining the proportions of phenotypes, the two species should show parallel variation. They do not. Cain and Sheppard argue that this result does not necessarily contradict their hypothesis. The consequences of visual predation may be influenced by the non-visual selective values of the various phenotypes, values that are unlikely to be the same in both species. Small differences in ecology or behaviour might also result in a different pattern of selection, even from the same predator.

The work described in this paper is a study of the distribution of phenotypes in natural populations of *Cepaea hortensis* and an attempt to make clear the differences between its polymorphism and that of *Cepaea nemoralis*.

2. METHODS

During 1957 and 1958, I collected random samples of *C. hortensis* from sixty-four colonies, most of them within sixty miles of Oxford. Localities were selected for diversity of vegetation and background. Where possible, several widely separated habitats of the same type were studied. During sampling the area was searched carefully to avoid collecting only those snails that were most obvious to the eye.

The snails were scored for age, condition (live, dead predated, or dead unpredated), colour and banding :—

(i) Age

Snails whose lips had not yet formed were classed as juveniles. Those with complete or incomplete lips were considered to be adult.

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(ii) Condition

In order to prevent duplication, broken shells were scored only if they displayed more than half the lip. Shells broken by thrushes could usually be distinguished from those predated by small mammals (see Morris, 1954).

(iii) Colour

In *C. hortensis* the colour of the shell varies from almost pure white to a very dark greenish-black, but the commonest colours are white, yellow, pink and brown (see Taylor, 1914). The first two colours (var. *alba* Picard and var. *lutea* Picard) are often difficult to separate, and appear to have every sort of intermediate between them. I have included them both in the " yellow " class. The pink forms (var. *incarnata* Picard) and the " browns " (var. *baudonia* Moquin-Tandon and var. *olivacea* Taylor) can more easily be distinguished. Shells of the latter group have a pale violet ground-colour which is modified by the overlying periostracum so that they appear brown. It is probable that Taylor's var. *lilacina* is a brown that has a very pale periostracum.

(iv) Banding

The shell may have up to five bands running along the whorls (very rarely six or more). The bands are usually dark brown in colour. A form in which they
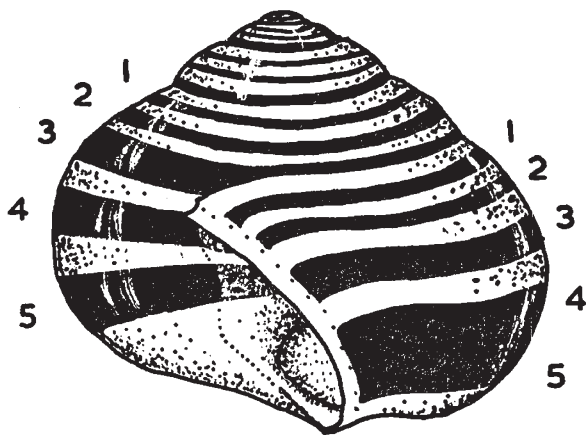

FIG. 1.—A shell of *C. hortensis*, showing the method of numbering the bands. On the right-hand whorl, bands 4 and 5 are fused.

are translucent and unpigmented on a pale yellow or white ground-colour (var. *arenicola* MacGillivray) occurs among my collections, usually as a distinct type. In some samples, however, there is a general tendency for the bands to be pale or partially pigmented (var. *lurida* Moquin-Tandon), and intermediates occur between normal banding and the unpigmented condition. Collections showing more than 10 per cent. of such forms are recorded with an asterisk, but the individual shells, unless completely unpigmented, are scored as normal.

For recording, the bands are numbered 1, 2, 3, 4 and 5 from the top of the whorl downwards (see fig. 1). Absence of a band is recorded by 0, and fusions are signified by bracketing the numbers representing the fused bands (*e.g.* (12)3(45), 023(45) etc.). Following Cain and Sheppard (1950) I have not regarded bands as fused unless they are joined for at least 90° round the whorl from the lip. Fusions are not scored in young snails. Bands occurring only as a faint trace near the lip are not recorded as present. They are very rare.

I have grouped the habitats from which samples were taken into six classes.

(i) *Grass*. This includes open chalk downlands as well as a number of roadside habitats in which grass predominates. The background is usually a uniform light green. In long grass it may be darker, but still fairly uniform.

(ii) *Hedgerows and rough herbage*. This class comprises open roadside habitats in which grass does not predominate. The vegetation is often mixed, and may include nettles (*Urtica dioica* L.), brambles (*Rubus* sp.), willowherb (*Epilobium* spp.), ivy (*Hedera helix* L.), hawthorn and various umbellifers. The background is generally darker and less uniform than in the grassy habitats.

(iii) *Beechwoods*. These are all escarpment woods of pure beech, or beech and ash. *C. hortensis* is not common within them, but tends to occur where there is some ground vegetation. The collections from Maidensgrove and Savernake were taken in patches of rosebay willowherb (*Epilobium angustifolium* L.), those from Clipper Down, Hackpen and Aston Rowant in stinging nettles, and the Ward's Hurst sample was collected from low brambles. The Knoll Down group are small beech clumps—each less than a hundred yards across, and each surrounded by downland grass. At Knoll Down B the ground flora within the clump itself is predominantly grass. There is less grass at Knoll Down A, and hardly any at all in Knoll Down C. In the beechwood areas, whatever the ground vegetation, there is a layer of leaf-litter which gives a dark background. I have not found *hortensis* in plateau beech-woods, although *nemoralis* is often present.

(iv) *Other deciduous woods*. This is a heterogeneous class, including all those woods that do not fit into the last category. Boarstall Wood is predominantly oak, Uffington is oak and hawthorn. Derry Hill Great Wood is open beech with ash and conifers. Wychwood, Rockley Copse, Guiting Wood and Elsfield Covert are very mixed, with hawthorn, oak, ash and hazel. Elsfield Covert, in addition, is damp and boggy, with clumps of *Equisetum*. In all cases the snails were collected in areas of dense ground vegetation, generally either willowherb or nettles. The background is usually less dark and less uniform than in the beechwood areas. Elsfield, however, is very dark indeed.

(v) *Fens*. Samples were taken in three calcareous fens. The collecting areas at Marcham and Headington Wick are in long rushes, and the backgrounds are uniform dark brown. Shippon is greener and much more varied, with grass, nettles, and other herbage.

(vi) *Ivy*. The collections included here were taken beneath ivy (*Hedera helix* L.). The background is very dark brown, almost black ; the earth being bare and shaded by a close cover of ivy leaves. Beckley is the most uniform habitat. At Cassington and Mickleham the areas of ivy are fringed by grass. At Mickleham and Woodcote there is some penetration of the cover by umbellifers. The Sonning sample was collected from a bank of ivy within a mixed beech and ash wood.

3. RESULTS

The composition of samples is given in tables 1 and 2. Only live and predated adults are included. Young shells are not used in the tables because fusions of bands cannot be scored among them. Unbroken dead adults are excluded because the mode of death is not known, and therefore the direction of possible errors cannot be predicted (see below). Furthermore, in one colony—Dragons Hill—the dead unbroken shells showed a significantly higher proportion of banded forms than did the live adults ($p < 0.005$).

Among my samples, no significant differences were observed between live and predated adults. This does not, of course, argue against the hypothesis of visual selection by predators. A force of

TABLE 1—*The composition of*

(a)	(b)				(c)		(d)		(e)		(f)	(g)	(h)
	Yellows				Pinks		Browns		A				
Locality	12345	00300	00000	Others	12345	00000	12345	00000	12345	Others	var. lurida	Shells with fusions	Total
Grass													
1. Silbury Hill, A	159	...	70	2	...	...	27	2	...	...	...	143	260
2. Silbury Hill, B	83	...	32	...	...	...	5	2	...	...	...	50	122
3. Silbury Hill, C	46	...	41	...	...	2	2	...	...	...	...	12	91
4. Silbury Hill, D	53	...	23	...	...	...	1	1	...	...	...	5	78
5. Dragons Hill	60	...	259	4	...	...	...	...	...	...	...	25	323
6. Walker's Hill	7	...	22	...	...	...	...	1	...	...	...	1	30
7. Morgan's Hill	14	...	9	4	...	10	...	...	...	...	*	10	37
8. Three Barrows	19	...	55	...	...	...	3	2	...	...	...	7	79
9. The Ball, Pewsey	29	...	32	...	4	...	...	...	...	...	...	10	65
10. Chisledon-Ogbourne	161	...	142	6	...	7	3	2	4	...	...	5	325
11. Wheatley	80	...	48	1	...	...	...	4	...	...	...	18	133
12. Cowley-Chislehampton	21	...	...	...	...	5	...	4	...	...	...	...	30
13. Wooton-Abingdon A	51	...	35	2	...	8	...	...	1	...	...	4	97
14. Woodperry Corner	37	...	28	...	...	...	...	...	6	...	*	5	71
15. Wheatley-Holton	51	...	32	5	...	...	...	...	...	...	...	10	88
16. Kingstone Coombes	41	...	1	2	...	...	...	...	...	...	...	24	44
17. Etchilhampton	18	...	30	...	...	...	...	...	...	...	...	9	48
18. Kingston Bagpuize-Standlake	11	...	11	1	...	1	...	...	...	...	...	3	24
19. Watlington Hill	...	...	6	...	...	...	...	...	...	...	...	...	6
20. Forest Hill-Stanton	8	...	13	...	...	...	...	...	...	...	...	...	21
Total	949	...	889	27	4	33	41	18	11	...	2	340	1972
Hedgerows and Rough Herbage													
1. Cumnor	43	...	7	1	...	...	...	...	1	...	*	6	52
2. Wootton Rivers	17	...	...	...	2	2	...	1	...	...	*	1	22
3. Marston-Elsfield	22	...	...	...	...	...	...	...	4	...	*	6	26
4. Stowood Crossroads	25	2	8	1	...	2	...	2	1	...	...	6	41
5. Oare Hill A	133	...	14	65	...	...	...	...	...	...	*	27	212
6. Oare Hill B	5	...	...	...	...	...	...	...	...	...	...	1	5
7. Derry Hill A	30	...	9	...	...	3	...	...	2	...	...	8	44
8. Rockley, Berks	17	2	9	1	...	4	...	...	...	...	...	3	33
9. Wooton-Abingdon B	136	21	52	5	...	10	...	...	5	1	*	14	230
10. Swerford	46	...	12	1	...	...	...	...	...	...	...	26	59
11. Christmas Common	7	...	38	...	...	...	...	...	2	...	...	...	47
12. Fiddler's Hill	174	...	39	16	...	...	...	...	...	...	*	1	229
13. Springhill	13	...	...	...	...	...	...	...	1	...	*	...	14
14. Ashbury Hill	4	...	...	3	...	...	...	...	12	9	*	1	28
15. Derry Hill B	6	...	7	...	...	12	...	...	...	...	...	2	25
Total	678	25	195	93	2	33	...	3	28	10	8	102	1067

random samples of C. hortensis.

(i)	(k)	(l)	(m)	(n)	(o)	(p)	(q)
Per cent. Yellows (inc. A)	Per cent. Pinks	Per cent. Browns	Per cent. A	Per cent. "Effectively unbanded"	Per cent. Y_{00000}	Per cent. Fusions in 12345 and others	Further details
							A = var. *arenicola*
88·8	...	11·2	...	27·7	26·9	76·1	2-10345
94·3	...	5·7	...	27·9	26·2	56·8	
95·6	2·2	2·2	...	47·3	45·1	25·0	
97·4	...	2·6	...	30·8	29·5	9·4	
100·0	...	...	...	80·2	80·2	39·1	4-10345
96·7	...	3·3	...	76·7	73·3	14·3	
73·0	27·0	...	...	51·4	24·3	55·6	3-00345, 1-02345
93·7	...	6·3	...	72·2	69·6	31·8	
93·8	6·2	...	...	49·2	49·2	30·3	
96·3	2·2	1·5	1·2	48·0	43·7	2·9	2-10345, 1-12045 2-02345, 1-00345
97·0	...	3·0	...	39·1	36·1	22·2	1-10345
70·0	16·7	13·3	...	30·0	...	...	All pinks have black lips
90·7	9·3	...	1·0	45·4	36·1	7·4	2-10345 All pinks have black lips
100·0	...	...	8·5	47·9	39·4	11·6	
100·0	...	...	...	36·4	36·4	17·9	3-10345, 2-00345
100·0	...	...	...	2·3	2·3	55·8	2-10345
100·0	...	...	...	62·5	62·5	50·0	
95·8	4·2	...	...	50·0	45·8	25·0	1-10345. Pink has brown lip
100·0	...	...	...	100·0	100·0	25·0	Per cent. fusions scored from unpredated dead
100·0	...	...	...	61·9	61·9	...	
100·0	...	...	1·9	14·8	12·9	13·3	1-12045
77·3	18·2	4·5	...	22·7	...	5·3	
100·0	...	...	15·4	15·4	...	23·1	
90·2	4·9	4·9	2·4	36·6	19·6	22·2	1-02300
100·0	...	...	...	17·5	6·6	16·3	15-10345, 3-00345, 1-00340, 11-10045, 16-10005, 16-00005
100·0	...	...	...	...	...	20·0	
93·2	6·8	...	4·5	31·8	20·5	25·0	
87·9	12·1	...	...	45·5	27·3	16·7	All pinks have black lips 1-10345
95·7	4·3	...	2·6	38·7	22·6	9·5	All pinks have black lips 4-10345, 1-12045, 1-A00300
100·0	...	...	...	20·3	20·3	55·3	1-12305
100·0	...	...	4·3	85·1	80·8	...	
100·0	...	...	...	17·0	17·0	0·5	1-02345, 1-10045, 11-10345, 3-00345
100·0	...	...	7·1	7·1	...	...	
100·0	...	...	75·0	75·0	...	3·6	3-10345, 9-A10345
52·0	48·0	...	...	76·0	28·0	33·3	

TABLE 2—*The composition of*

(a)	(b)				(c)		(d)		(e)		(f)	(g)	(h)
	Yellows				Pinks		Browns		A				
Locality	12345	00300	00000	Others	12345	00000	12345	00000	12345	Others	var. lurida	Shells with fusions	Total
Beechwoods													
1. Clipper Down Wood	86	...	4	...	...	...	...	...	...	...	*	58	90
2. Hackpen Wood	36	...	5	2	...	...	...	...	...	...	...	8	43
3. Kingstone Coombes	21	...	...	...	...	...	...	...	...	...	...	7	21
4. Danks Down Wood	33	...	8	...	...	...	...	...	...	...	...	16	41
5. Fawley Bottom Wood	8	...	1	...	...	...	...	...	...	...	*	3	9
6. Maidensgrove Wood	9	...	...	1	...	...	...	...	...	...	*	6	10
7. Ward's Hurst Wood	16	...	1	...	...	...	...	...	...	...	...	12	17
8. Aston Rowant Wood	4	...	3	...	...	...	...	7	...	...	...	2	14
9. Savernake Wood	7	...	...	...	...	...	...	...	...	...	...	3	7
10. Rockley Wood	18	...	...	...	...	...	...	...	...	...	...	9	18
11. Manton Wood	8	...	2	...	...	...	...	1	...	...	...	1	11
12. Knoll Down A	29	...	26	...	...	...	...	...	...	...	...	20	55
13. Knoll Down B	10	...	10	...	...	...	...	...	...	...	...	6	20
14. Knoll Down C	12	...	1	...	...	...	...	...	...	...	...	6	13
Total	297	...	61	3	...	...	...	8	...	...	3	157	369
Other Deciduous Woods													
1. Boarstall Wood	17	4	15	...	...	...	1	34	1	...	...	3	72
2. Rockley Copse	60	17	11	...	...	92	...	...	...	...	...	8	180
3. Guiting Wood	11	...	2	...	...	...	...	...	...	...	...	1	13
4. Wychwood Forest	4	...	1	...	3	...	...	...	...	...	...	3	8
5. Uffington Wood	40	...	3	2	...	...	...	...	1	...	*	15	46
6. Derry Hill Great Wood	13	...	8	...	...	7	...	...	...	...	...	9	28
7. Elsfield Fox Covert	12	5	13	...	...	15	...	...	...	...	...	10	45
Total	157	26	53	2	3	114	1	34	2	...	1	49	392
Fens													
1. Shippon	26	...	40	...	...	13	...	...	...	...	...	1	79
2. Marcham	9	...	17	...	...	8	9	11	...	...	...	10	54
3. Headington Wick	33	...	28	...	...	...	...	1	...	...	...	19	62
Total	68	...	85	...	...	21	9	12	...	...	...	30	195
Ivy													
1. Mickleham, Surrey	55	...	26	...	10	6	...	1	...	...	*	37	98
2. Cassington	19	...	3	...	...	...	...	...	...	...	...	13	22
3. Beckley	31	...	...	...	...	...	...	11	...	...	...	25	42
4. Woodcote	18	...	1	...	...	...	...	...	...	...	*	12	19
5. Sonning-on-Thames	11	...	8	...	4	5	5	11	...	...	...	18	44
Total	134	...	38	...	14	11	5	23	...	...	2	105	225

random samples of C. hortensis *(continued)*.

(i)	(k)	(l)	(m)	(n)	(o)	(p)	(q)
Per cent. Yellows (inc. A)	Per cent. Pinks	Per cent. Browns	Per cent. A	Per cent. "Effectively unbanded"	Per cent. Yooooo	Per cent. Fusions in 12345 and others	Further details
							A = var. *arenicola*
100·0	...	...	...	4·4	4·4	67·4	
100·0	...	...	...	11·6	11·6	21·1	2-12045
100·0	...	...	...	...	...	33·3	
100·0	...	...	...	19·5	19·5	48·5	
100·0	...	...	...	11·1	11·1	37·5	
100·0	...	...	...	...	...	60·0	1-023(45)
100·0	...	...	...	5·9	5·9	75·0	
50·0	...	50·0	...	71·4	21·4	50·0	
100·0	...	...	...	...	...	42·9	
100·0	...	...	...	...	...	50·0	
90·9	...	9·1	...	27·3	18·2	12·5	
100·0	...	...	...	47·3	47·3	77·0	
100·0	...	...	...	50·0	50·0	60·0	
100·0	...	...	...	7·7	7·7	50·0	
51·4	...	48·6	1·4	75·0	20·8	15·8	
48·9	51·1	...	...	66·7	6·1	13·3	All pinks have black lips
100·0	...	...	...	15·4	15·4	9·1	
62·5	37·5	...	...	12·5	12·5	42·9	
100·0	...	...	2·2	8·7	6·5	34·9	2-10345
75·0	25·0	...	...	53·6	28·6	69·2	
66·7	33·3	...	...	73·3	28·9	83·3	
83·5	16·5	...	...	67·1	50·6	3·8	All pinks have black lips
48·1	14·8	37·0	...	66·7	31·5	55·6	All pinks have black lips
98·4	...	1·6	...	46·8	45·2	57·6	
82·7	16·3	1·0	...	33·7	26·5	56·9	
100·0	...	...	...	13·6	13·6	68·4	
77·5	...	22·5	...	22·5	...	80·6	
100·0	...	...	...	15·9	5·3	66·7	
43·2	20·4	36·4	...	54·5	18·2	90·0	

selection sufficient to account for the observed differences in the
distribution of phenotypes *between* populations would not show itself
within them unless the samples of both live and predated adults were
very large indeed.

If the data given in tables 1 and 2 are compared with Cain and
Sheppard's (1954) results for *Cepaea nemoralis* from the same region, it
is seen that the two species differ profoundly in the distribution of their
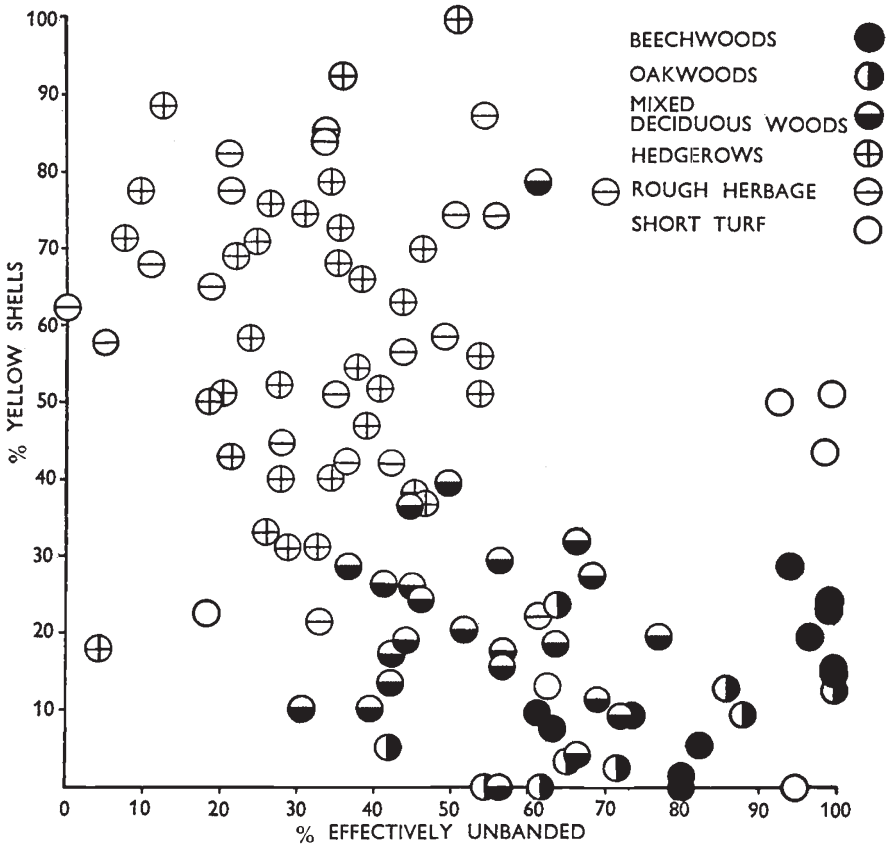
FIG. 2.—*C. nemoralis*. A scatter-diagram showing the relation between percentage of
yellow shells, percentage of " effectively unbanded " shells, and the nature of the
habitat (after Cain and Sheppard, 1954).

phenotypes. In *hortensis* there is far less variation in the proportion of
yellow shells. In nearly every case they form the greater part of the
population (columns (*b*) and (*i*)). Albino shells (var. *arenicola*) are
more common than in *nemoralis* (columns (*e*) and (*m*)), as are pale-
banded forms (column (*f*)) and banded browns (column (*d*)). Banded
pinks, on the other hand, are much rarer.

The tables show also that the distribution of phenotypes is not
random with respect to habitat. Grasslands, for instance, tend to have
a higher proportion of unbanded shells than beechwoods (see column

(n)). The converse is true in *C. nemoralis*. Figs. 2 and 3 show this clearly.

Fig. 2 is the scatter-diagram given by Cain and Sheppard (1954). Each spot represents one colony of *nemoralis*. The position of a spot along the vertical axis is determined by the percentage of yellow
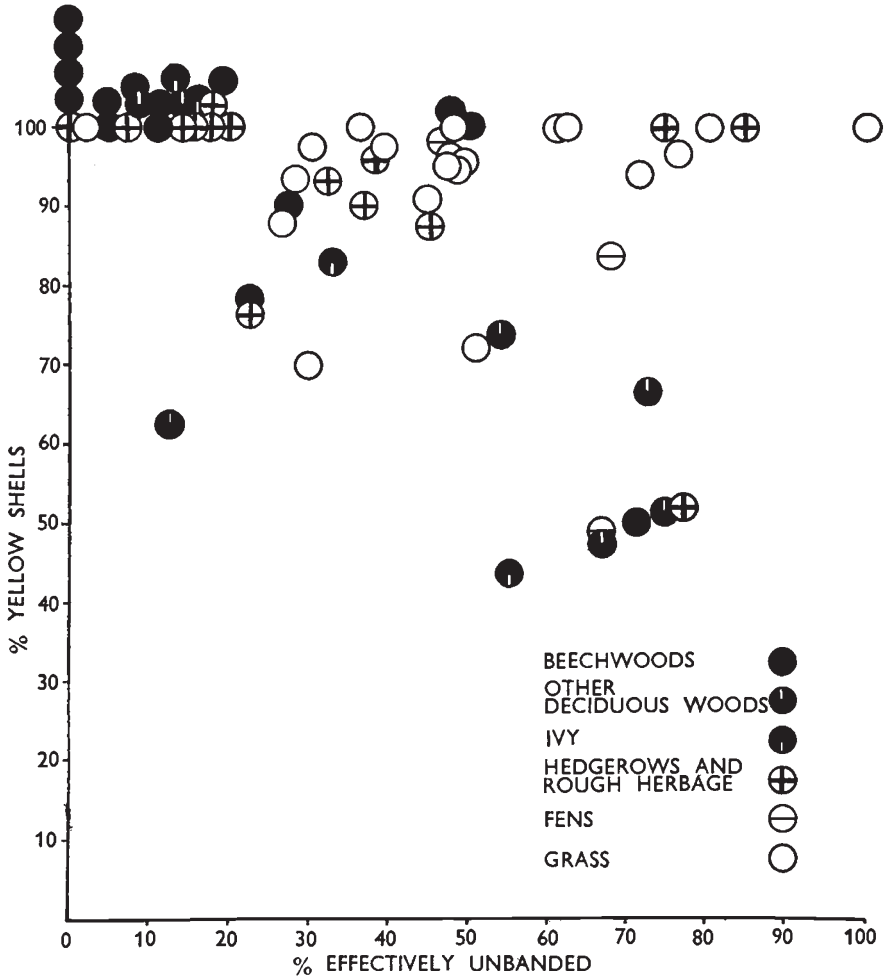
FIG. 3.—*C. hortensis*. A scatter-diagram similar to fig. 2, showing the different distribution of phenotypes in this species.

shells in the colony. Along the horizontal axis its position is determined by the percentage of " effectively unbanded " shells (*i.e.* those shells that have the top two bands missing, including 00300, 00345, 00045, 00000, etc.). On the diagram, colonies from each habitat class tend to be grouped together. The beechwoods lie at the lower right-hand corner, having a low proportion of yellow and a high proportion of unbanded shells. The more open habitats, such as hedgerows and rough herbage, tend towards the left-hand corner. It

must be noted that Cain and Sheppard (1954) class hedgerows and rough herbage as separate groups, but include grasslands in the latter category.

Fig. 3 is a similar diagram, drawn for my collections of *C. hortensis*. Although there is some separation between habitat classes, the grouping
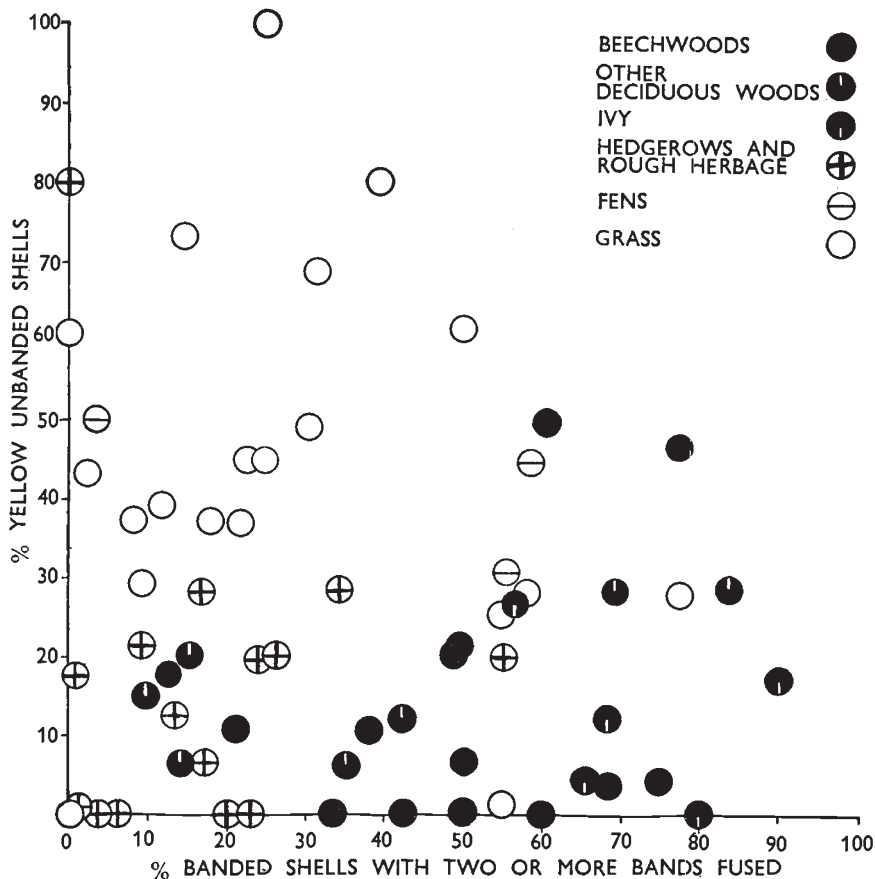
Fig. 4.—*C. hortensis*. A scatter-diagram showing the relation between percentage of yellow unbanded shells, percentage of banded shells with fused bands (see text) and the nature of the habitat.

here is much less distinct. Furthermore, the beechwoods tend to fall on the left-hand side, and the grasslands on the right.

Tables 1 and 2 show that the greater part of the variation of *C. hortensis* is within the yellow colour class. Fig. 4, another scatter-diagram, makes allowance for this. Along the vertical axis are plotted the percentages of yellow unbanded shells (tables 1 and 2, column (*o*)). The horizontal axis gives the proportions of banded shells that have two or more bands fused together (tables 1 and 2, column (*p*)). These proportions are expressed as percentages of the numbers of shells that *could* have two or more bands fused (*i.e.* shells with bands next to

each other—including such forms at 12345, 10045, 12045, 00345, etc., but excluding 00000, 00300, 10005, 10305, etc.).

Fig. 4 shows a clear separation into colour classes. The woodlands, which have few yellow unbanded shells and a high proportion of fusions, are almost completely distinct from the grasslands. The hedgerows and rough herbage, as might be expected, take up a more or less intermediate position. The samples taken under ivy, the darkest habitat, have high percentages of fusions.

The three figures show clearly that *hortensis* populations respond to the influence of the habitat, but that the response is very different from that of *nemoralis*.

4. RELIABILITY OF RESULTS

The results obtained might be affected by several possible errors:

(i) There are, no doubt, random errors of sampling. They would not, of course, give the systematic differences that have been observed between habitat classes. The significance of these differences can easily be demonstrated by non-parametric methods. The samples are arranged in order according to the percentage of shells displaying a particular character, and the distribution of habitat classes about the median percentage is tested by χ^2, the null hypothesis being that, in each habitat, there should be equal numbers of samples falling on either side of the median. For the two characters used in fig. 4 it is found that beechwoods, other deciduous woods, and ivy do not differ significantly from one another and that therefore they can be grouped together for comparison with the other two major classes (hedgerows, rough herbage and grasslands). The distributions of both the percentage of yellow unbanded and the percentage of fusions give 3×2 tables with probabilities that are less than one in a thousand. More refined statistical treatments give even lower values.

(ii) I may have collected too high a proportion of shells that appear conspicuous to the eye. There is no doubt, however, that yellow unbanded shells are more obvious against the dark background of woodlands than are pink, brown, or banded forms—and that shells with their bands fused together are more difficult to see in such situations than are banded shells without fusions. Furthermore, in uniform green grass or herbage the yellow unbanded forms are less obvious than the banded ones, particularly less so than shells with fused bands. Thus any errors of selection by the collector could only tend to obscure the observed differences between habitat classes. This applies also to samples of broken shells collected by thrushes.

(iii) Schnetter and Sedlmair (1953) and Sedlmair (1956) claim to have detected differences in behaviour under experimental conditions between various phenotypes of *Cepaea*. Banded forms of *hortensis*, for instance, were significantly more active than unbanded when the humidity was high. In dry conditions the activity of the unbanded

TABLE 3

Comparison of samples taken from the same places at different times (see text).

Locality	Y	P	B	12345	F	Total	Date	Comments
Uffington Wood . .	46	o	o	43	15	46	12.6.57	L.
	21	o	o	20	6	21	5.6.58	L.
Boarstall Wood . .	22	o	19	8	o	41	8.6.57	L.
	15	o	16	11	3	31	1951	T., Cain & Sheppard
Clipper Down Wood .	63	o	o	61	42	63	10.6.57	L.
	27	o	o	25	16	27	10.6.57	T.
Kingstone Coombes Wood	19	o	o	18	5	19	1951	T., Cain & Sheppard
	21	o	o	20	7	21	29.5.57	T.
Rockley Copse . .	19	26	o	13	2	45	1952	T., Cain & Sheppard
	63	61	o	43	5	124	14.6.57	T.
Shippon Fen . . .	45	9	o	17	1	54	22.3.57	L.
	531	84	o	259	16	615	21.3.59	T.
Wooton-Abingdon Road .	113	6	o	73	5	119	30.4.57	L.
	107	4	o	73	7	111	4.5.57	L.
Oare Hill . . .	191	o	o	178	26	191	1950	L., Cain & Sheppard
	21	o	o	20	1	21	6.6.57	L.
Shepherd's Rest . .	227	o	o	193	7	227	1957	L., Sheppard
	19	o	o	19	0	19	14.4.58	L.
Wheatley Bridge . .	63	o	2	39	8	65	10.4.57	L.
	66	o	2	42	10	68	10.4.57	M.
Dragons Hill . . .	169	o	o	31	11	169	16.9.56	L.
	54	o	o	9	5	54	16.4.57	L.
	62	o	o	14	8	62	16.4.57	M. & T.
	24	o	o	6	0	24	12.6.57	L.
	34	o	o	6	4	34	16.4.58	L.
	43	o	o	6	4	43	15.4.59	L.
	36	o	o	9	4	36	15.4.59	M. & T.
Silbury Hill, C . .	87	2	2	48	9	91	6.6.57	L., V.S.
	260	1	10	151	69	271	17.6.58	L., V.C.
	62	1	4	38	16	67	2.9.58	L., Reynolds, V.S.
	224	o	2	116	37	226	24.10.58	L., Paterson & Murray
	143	o	5	77	31	148	20.4.59	·L., V.S.
Silbury Hill, 8 . .	72	o	10	59	43	82	17.7.57	L.
	17	o	o	12	9	17	14.9.58	L.
White Horse Hill, 1 .	33	o	o	31	9	33	16.4.58	L.
	52	o	o	52	12	52	15.4.59	L.
Little Hinton . . .	33	o	o	25	4	33	19.4.59	T. (new shells)
	28	o	o	24	4	28	19.4.59	T. (old shells)
Fyfield Roadbank, 1 .	113	o	o	52	11	113	6.58	L., Armstrong
	84	o	o	39	7	84	6.58	L., Armstrong
	44	o	o	27	5	44	6.58	L., Armstrong
	58	o	o	34	8	58	6.58	L., Armstrong
	32	o	o	18	4	32	20.4.59	L. On ground
	57	o	o	27	8	57	20.4.59	L. Climbing
	80	o	1	31	14	81	20.4.59	L.
Fyfield Roadbank, 2 .	41	o	o	20	2	41	6.58	L., Armstrong
	39	o	o	17	3	39	6.58	L., Armstrong
	49	o	o	26	8	49	6.58	L., Armstrong
	57	o	o	27	6	57	6.58	L., Armstrong
Fyfield Roadbank, 3 .	70	o	10	44	26	80	1.7.57	L.
	51	o	4	34	19	55	1.7.57	T.
	21	o	3	6	3	24	24.9.57	L.
	58	o	5	34	20	63	24.9.57	T.

variety seemed to be greater, although in this case the difference was not statistically significant. Such experiments do not necessarily reflect what happens in natural populations, but they do show that environmental influence *could* introduce systematic errors into the samples. I have searched for effects of this sort, comparing collections taken from the same colony at various times, under various weather conditions. Table 3 summarises the results of these comparisons. I have included a number of samples that were collected after tables 1 and 2 had been drawn up. Full details of their composition will be recorded elsewhere.

In two localities (Silbury Hill C, and Fyfield Roadbank 3) there were apparent significant heterogeneities between successive samples, but an overall summation of χ^2 (table 4) shows that this extent of

TABLE 4

Sums of χ^2 comparing samples taken from the same colonies at different times—calculated from data of Table 3.

	Banding	Fusions	Colour
Total χ^2 . . .	29·31	33·30	12·58
Degrees of freedom .	35	35	13
Probability . . .	> 0·5	> 0·5	> 0·25

heterogeneity does not in fact exceed chance expectation. In none of the three classes (banding, fusions and colour) does the overall probability fall below 0·25.

I have also compared, in the field, samples taken from the stems and leaves of tall herbage with collections taken from the ground beneath them. As these comparisons were made on the spot, no figures are available, but in fifteen tests no significant differences were observed. It seems that differential behaviour does not significantly and directly alter the composition of samples, although it might well affect the selective advantages of varieties in a population.

We must conclude that the observed grouping of samples from similar habitats represents a genuine influence of the environment upon the composition of *hortensis* populations. This influence could be the result either of direct action by environment upon the phenotype of individual snails, or of natural selection acting upon genetically determined differences—or of both.

5. GENETICS

Many of the obvious colour and banding varieties of *Cepaea* are known to be genetically determined. *C. hortensis* has been bred by Lang (1904, 1912) and *C. nemoralis* by Lang (1908, 1911, 1912), Lamotte (1951, 1954) and Cain and Sheppard (1957). In *hortensis*, as in *nemoralis*,

absence of banding is dominant to its presence, and pink is dominant to yellow (Lang, 1904). The inheritance of brown colour in *hortensis* is not known although, by analogy with *nemoralis*, brown may be expected to dominate pink and yellow. Lang's results suggest that band-fusions may be inherited. Boettger (1950) states that the different combinations of fused bands form an allelic series, but unfortunately he does not provide the necessary data. Forms with thin, interrupted bands are reported to be dominant to the more common thick-banded varieties (Lang, 1912). Lang gives no information, however, about the inheritance of the unpigmented or partially pigmented conditions— although he has shown the former to be recessive in *nemoralis* (1911). Phenocopies, as far as I know, have not been reported by reliable observers.

6. NATURAL SELECTION

Among populations of organisms, spatial or temporal differences in the proportions of genetically determined varieties can be due either to random or to directed processes (see, for instance, Wright, 1955). While " random drift " could, no doubt, occur within populations of *hortensis*, the systematic differences between habitat classes indicate the action of natural selection.

Sheppard (1951) has demonstrated the selection of colour varieties in two populations of *C. nemoralis*. He showed that the percentage of yellow snails killed by thrushes decreased from the middle of April until the middle of May. He gave evidence that this was the result neither of changes of feeding grounds by the thrushes, nor of variations in the populations from which they were collecting. The most obvious explanation was that the thrushes could see the yellow snails less easily as the background became greener.

Goodhart (1958*b*) reports similar seasonal differences in the proportions of pink and yellow *hortensis* collected by thrushes. His data cannot be considered as *conclusive* evidence of selection, for the following reasons:

(*a*) The population from which the birds were collecting was not sampled.

(*b*) The habitat was heterogeneous, and Goodhart did not exclude the possibility of seasonal changes of feeding ground.

(*c*) He compared the proportions of varieties found around " thrush stones " during five successive summers with those collected during the intervening winters. The proportion of pink shells in the two groups appeared to be significantly different ($p < 0.01$). The final summer, however, showed a significantly higher proportion of pinks than the other summers ($p < 0.01$), and ought not to have been included with them. When it is excluded, the difference between summers and winters is no longer significant ($p > 0.05$).

I have criticised Goodhart's work because the hypothesis of visual selection, if it is to be accepted, must be based upon unequivocal

results. Nevertheless, for the reasons given below, it seems very likely that thrushes do, in fact, tend to select the most obvious varieties of *hortensis*, and to overlook those that resemble the background. Shells of this species are found on thrush stones as commonly as are those of *nemoralis*. Both species have similar colour and banding patterns. Since selective predation has been demonstrated in *nemoralis*, it is reasonable to expect the same in *hortensis*.

Predation by thrushes is not, of course, the only possible form of selection. Many other birds eat snails, and they may act in a similar way. Small mammals also prey upon *Cepaea*, and Cain (1953) has suggested that, since they are colour-blind, selection may depend on tone rather than colour. Boettger (1954) and Sedlmair (1956) have reported differences in survival between various phenotypes of *hortensis* and *nemoralis* under adverse conditions. Komai and Emura (1955) have discovered comparable differences in *Bradybaena similaris*.

Polymorphism in *Cepaea* has been in existence since Neolithic times (Diver, 1929) and probably for much longer. The presence of similar colour and banding varieties, not only in all the species of *Cepaea*, but also in the related genus *Pseudotachea* (Sacchi, 1956) suggests that the polymorphism may be very ancient indeed. On a shorter time-scale, Goodhart (1956, 1958a) has shown that colonies may persist virtually unaltered in their phenotypic constitution for periods exceeding fifty years. Monomorphic colonies are rare. These facts suggest that much of the variation in *Cepaea* comes into the category of balanced, rather than transient, polymorphism (as defined by Ford, 1945).

For the maintenance of polymorphism there must be forces acting so that the rarer a gene becomes, the greater is its relative advantage. Such a situation occurs if the heterozygote tends to produce relatively more descendants than either homozygote. Another means of maintaining diversity may be provided by predators. If they come to associate common colour varieties with food, they may overlook the rarer forms, even if these stand out against their background. Evidence of effects of this sort is found in the works of Popham (1941, 1942) and Reighard (1908) on predation by fishes.

7. DISCUSSION OF RESULTS

Fig. 3 shows that the distribution of *colour* varieties in *hortensis* is not obviously related to the background from which the samples were taken. The collections with the lowest proportions of yellow shells, however, come from habitats that appear, subjectively, to be the most acid. The snails from Aston Rowant, Boarstall, Marcham, Elsfield and Derry Hill were all collected in piles of rotting vegetation. At Rockley Copse there is not a great deal of dead plant matter, but the area is flat and sandy, with patches of bracken. The Sonning sample seems to be an exception, having been taken under ivy on a

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chalk scarp. With the evidence available, the relation between acidity and the incidence of pinks and browns cannot be accepted as fact. It remains an interesting possibility.

Whatever may be the solution of the problem of the distribution of colour varieties, one thing remains certain. *Cepaea hortensis*, in the majority of colonies, has proportionately far fewer pinks and browns than has *nemoralis*. It is remarkable that, in spite of this, the samples seem to match their background.

On dark brown uniform backgrounds, in woods and under ivy, there are high percentages of banded forms with their bands fused together (see fig. 4). The effect of band-fusions is to make the shell appear dark brown in spite of the yellow ground colour, and to make it far less obvious against a woodland background.

In habitats with mixed vegetation (hedgerows and rough herbage) there is a preponderance of unfused banded forms. The disruptive effect of the bands tends to conceal the shells against the criss-cross of stems.

On grass, a uniform light green background, the yellow unbanded forms are least obvious, and most common.

It cannot be expected that the habitat classes will be as distinct in *hortensis* as they are in *nemoralis*. In the first place, *hortensis* is not at all common in woods, with the result that the woodland samples are very small and presumably subject to large sampling errors. Secondly, where *hortensis* does occur it tends to inhabit places where there is a good deal of ground vegetation and where the background is somewhat mixed. *C. nemoralis*, on the other hand, is commoner in woods and often lives where there is little or no ground cover, and where the background is very uniform.

It is therefore surprising how accurate is the agreement between the phenotype-frequency of *hortensis* and the nature of the background. Many colonies that appear, on the evidence of their position on fig. 4, to be aberrant do in fact come from unusual habitats. The beech-woods Knoll Down A and B have an unusually high proportion of yellow unbanded shells but, as I have already mentioned, they are unusually grassy, and the background in places is almost green. The Morgan's Hill downland colony is small in area, isolated and extremely exposed (on the crest of an 800 ft. hill). It has an unusually high percentage of fusions, but nine-tenths of these involve the lower two bands, which are not obvious when the snail is in its normal position on the ground. When a snail is climbing on vegetation the lower bands may be exposed; but at Morgan's Hill none of the plants were more than six inches tall. The distribution of different types of band-fusions will be discussed in a further paper.

The downland sample from Kingstone Coombes, which falls on fig. 4 among the beechwoods, was collected in a small patch of thistles about a hundred yards from a beechwood. Only *nemoralis* occurred in the surrounding grass.

The Cowley-Chislehampton colony, which has no yellow unbanded shells, remains a puzzle. It is small in area, surrounded by colonies of *nemoralis*, and one of its phenotypes, pink unbanded with black lip, is not characteristic of the region (see below). It is conceivable that this colony resulted from the introduction of a very few individuals from elsewhere. The question must, however, be left open.

The Christmas Common hedgerow has a very high proportion of yellow unbanded shells, but it is surrounded by downland, which comes within fifty yards of it. Nearby woods seem to contain only *nemoralis*. It is therefore possible that the unusually high percentage of yellow unbanded shells may be due to gene-flow from the downland.

The explanation of aberrant colonies in terms of gene flow must not be accepted uncritically. It can only be used if the colonies are small in area and numbers, and if the only possible gene flow is from larger colonies of the type to which the smaller ones tend. These conditions are fulfilled in the colonies from Kingstone Coombes and Christmas Common, but there are certainly factors other than background that affect the distribution of phenotypes. Exposure, or something related to it, seems to be one (Clarke, in preparation).

In spite of the two or three colonies that seem not to match their background, the agreement among the other sixty-two or three is very good indeed (see fig. 4).

There are a number of other phenomena, for which complete explanations have not yet been found:

(*a*) Both albinos (var. *arenicola*) and pale-banded forms (var. *lurida*) appear to be more common among hedgerows and rough herbage than they are elsewhere (see tables 1 and 2, columns (*e*) and (*f*)). If only the four major habitat classes are considered, these differences are significant at the 5 per cent. level.

(*b*) In the Oxford region, there are geographical differences in the distribution of certain phenotypes. There is an area of *hortensis* colonies near Abingdon, Berkshire—comprising about twenty square miles and bounded by the villages of Cumnor, Eaton, Fyfield, Marcham, Sunningwell and the town of Abingdon—in which pink shells with black lips occur, but in which yellow shells with black lips have not been found. Black-lipped pinks seem to be absent elsewhere in the Oxford region (excepting, that is, the colony on the road between Cowley and Chislehampton).

The 00300 phenotype appears to be restricted to an area between Rockley and Abingdon, and to another between Oxford and Brill.

Neither black-lipped pinks nor 00300 have been found on the chalk Downs, or on the Chilterns or Cotswolds.

8. DIFFERENCES BETWEEN THE TWO SPECIES

C. nemoralis and *C. hortensis* are very closely related, but nevertheless distinct, species. They can usually be distinguished by shell size,

lip shape, body pigmentation and so on, but the only consistent differences are in the genitalia, particularly in the size and shape of the dart (see Taylor, 1914; Aubertin, 1927; Diver, 1940; and Lamotte, 1951). The chromosome numbers of the two species are identical (Perrot and Perrot, 1938). Hybrids have been obtained between them, but the fertility of crosses is very low (Lang, 1908; Kleiner, 1913). Small numbers of naturally occurring hybrids have been reported (Boettger, 1921), and the possibility of some gene flow between the two species cannot be ruled out.

The polymorphisms in *nemoralis* and *hortensis* are probably determined by genes at homologous loci. In all the experiments so far recorded the dominance relations of the genes for colour and banding are the same in both species. Furthermore, the work of Cain and Sheppard (1954, 1957) suggests that samples from natural populations can be a guide to linkage relations, at any rate in *nemoralis*. If this is true of *hortensis*, we may expect the genes for colour and banding to be linked in this species also, because in my samples the two characters are very significantly associated ($p < 0.001$). There is usually a deficiency of banded forms among the pinks and browns.

9. CONCLUSIONS

I have shown that the proportions of different phenotypes in populations of *C. hortensis* can be related to the habitat in which they live, and that this relation is necessarily the result of natural selection, probably of visual selection by predators. The same is true of *C. nemoralis* but, as we have seen, the response of populations to the environment differs in the two species.

If the genes controlling the polymorphisms of *nemoralis* and *hortensis* are homologous, as they appear to be, then the differences of response are, at first sight, puzzling. They can, however, be satisfactorily explained.

I have already pointed out that the two species have slightly different ecological preferences. It might be argued that the selective forces acting upon them are not strictly comparable, and that parallel variation is not to be expected. This can only partly be true. Mixed colonies are fairly common, and in these circumstances the distribution of phenotypes is not the same in each species. In fact, each responds to the environment in its own way (Clarke, in preparation). There might, of course, be differences in behaviour or micro-ecology within a single mixed colony. These could certainly affect the selective values of particular genes, but in visibly uniform habitats they are unlikely to alter the *visual* selective values. *Cepaea hortensis* occurs in a number of uniform beechwoods, in any part of which the brown unbanded variety would be visually superior to the yellow form with fused bands. The latter form is not completely brown; it shows a trace of yellow at the suture. Nevertheless it predominates. This suggests that the difference in response between the two species is due not merely to behavioural

or micro-ecological preferences that cause the two species to occur on visibly different backgrounds.

It has often been pointed out that the action of particular genes cannot be considered apart from their genotypic environment (see, for instance, Mayr, 1954, 1955) and it seems very likely that, for reasons which have nothing to do with the appearance of the shells, the genes for brown and pink are, on the average, less advantageous against the genotypic background of *hortensis* than they are against that of *nemoralis*. In other words, non-visual environmental factors could affect the selective values of the genes in ways that depended upon the genotypic background, producing a low proportion of pinks and browns in most populations of *hortensis*, and a higher one in most populations of *nemoralis*. Such effects could alter the results of visual selection. In beechwoods, for instance, predation by thrushes would act upon *nemoralis* to increase the proportion of brown or pink unbanded shells. *C. hortensis* does not produce a high percentage of browns or pinks, probably for the reasons mentioned above, and therefore the same selective agent would increase the proportion of yellow shells with fused bands. The visible effect, an overall brown appearance, is very similar in both species, but the means of obtaining it are different. The range of variation is more circumscribed in *Cepaea hortensis* than it is in *Cepaea nemoralis*, but both species undoubtedly respond to the colour and uniformity of the background.

This study is regarded as an example of the importance of the genetic environment in determining the selective values of particular genes. It accounts for Lamotte's (1951) inability to find a correlation between the phenotype frequencies of the two snails, and contradicts his thesis that selection is unimportant in determining the distribution of colour and banding varieties.

10. SUMMARY

1. Random samples were taken from a number of colonies of the polymorphic snail *Cepaea hortensis* Müll. Shells were scored for age, condition, colour and banding.

2. Analysis shows that the proportions of certain varieties can be related to the type of habitat from which the samples were taken. Colonies in woodlands tend to have a high proportion of banded shells with the bands fused together—a condition that gives an overall brown appearance which matches the background of brown leaf-litter. Colonies from grasslands, on the other hand, show a relatively high percentage of unbanded forms, which more closely resemble the uniform green background of grass. The differences between habitat classes are statistically very significant.

3. Works on the genetics of *Cepaea* are reviewed. Many of the colour and banding varieties are known to be genetically determined.

4. There is good evidence that the statistical differences between habitat classes are due to the action of natural selection, particularly

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of visual selection by predators, and that the variation comes into the category of balanced, rather than transient, polymorphism.

5. A comparison is drawn between the polymorphism of *C. hortensis* and that of the closely related species *C. nemoralis*, which has been studied by Cain and Sheppard. It is likely that the genes controlling the polymorphisms in the two species are homologous. The comparison shows that although populations of both snails respond to the influence of the habitat, they do so in very different ways. This difference of response is regarded as an example of the importance of the genetic environment in determining the selective values of particular genes.

6. The study provides an explanation of Lamotte's inability to find a correlation between the phenotype-frequencies of the two snails in mixed colonies, and contradicts his thesis that selection is unimportant in determining the distribution of colour and banding varieties.

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