VISUAL AND OTHER SELECTION IN *CEPAEA*: A FURTHER EXAMPLE

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Received 4.iv.73

SUMMARY

Populations of *Cepaea nemoralis* and *C. hortensis* have been sampled in a small area in north-west Worcestershire. No clear ecological separation between the two species is apparent.

Morphs of *C. nemoralis* that one would expect to vary in frequency between woods and open habitats on the basis of visual selection do so in the manner expected.

The variation shown by *C. hortensis* in the region is quite different and much reduced, compared with that of *C. nemoralis*. The expected differences between woods and open habitats still occur, however. Tests for any relations between morph-frequency and two other environmental variables (altitude and proximity to water) have been made. Only altitude shows such relations: unbanded in *C. hortensis* tends to rise in frequency with altitude and *listeria* in *C. nemoralis* may do so.

The Index of Polymorphism of *C. nemoralis* is always high if *C. hortensis* is present, but may be low if the latter is absent. Several mechanisms which could explain this are suggested. Linkage disequilibria are apparent in *C. nemoralis*. Banding is deficient in browns and at an excess in yellows, compared with pinks, in all habitats. It is concluded that the diversity of selective forces acting affectively on *Cepaea* populations, not random events, is responsible for the wide variation between them in morph-frequencies.

1. INTRODUCTION

DURING the last quarter of a century studies of the genetic variation of *Cepaea nemoralis* (L.) and *C. hortensis* (Mull.) have shown that great differences may exist between regions in the type of variation exhibited. One method of investigating the reasons for such differences is to compare numerous regions and attempt to discover any regularities which may exist. The present study was made to add one more to the rapidly lengthening list of such regions studied in Britain. The region was chosen solely on the basis that I happened to be living there, so that the choice was random as far as the snails are concerned.

The area studied is an approximate square of side 12 km, situated immediately south-west of Worcester (52° 12' N, 2° 11' W). It lies some 37 km west of the region studied by Currey, Arnold and Carter (1964) and is ecologically similar to it. The topography is undulating, the soil being cold, damp, heavy clay. The land is well wooded and much of the area is permanent pasture, though arable farming is by no means uncommon.

The work was pursued between late summer 1964 and early summer 1966.

2. METHODS

Random collections of *Cepaea* were made within areas of less than 30 m diameter. Snails are not common in the region and many of the collections

TABLE 1
Details of sites and of collections taken from them

Name of site	Grid reference	Habitat	Altitude	Water	<i>C. nemoralis</i>	<i>C. hortensi</i>
Caldewell Wood	914483	W	75	+	7	2
Clerkenleap	852514	W	50	+	0	16
Croome D'Abitot	888453	RH	125	—	10	55
Croome Perry Wood	903472	W	100	—	5	8
Deerfold Wood	909478	W	125	—	19	1
Dunstable	882431	H	50	—	8	0
Great Comberton	961429	H	100	—	1	19
Hatfield	868506	H	100	—	60	0
High Green 1	870457	RH	75	—	16	0
High Green 2	874457	W	75	—	17	0
Lower Wolverton	927501	W	100	+	45	0
Normoor	862474	W	75	+	10	27
Norton	893514	RH	125	—	26	1
Norton 2	893509	G	125	—	0	12
Pershore 1 and 2	952449	TH	50	+	0	44
Pirton 1	892470	H	75	—	9	0
Pirton 2	888471	H	100	—	18	1
Pirton 3	880479	W	175	—	7	0
Pirton Court	881465	H	100	—	12	0
Spetchley 1	890541	W	200	—	30	0
Spetchley 2	893541	H	200	—	23	0
Spetchley 3	900539	W	175	—	31	0
Spetchley Park 1	896531	W	150	+	5	0
Spetchley Park 2	891536	W	150	+	24	0
Stonebow	938498	H	100	+	26	0
Stoulton	909491	W	100	+	2	43
Swinesherd 1 and 2	879540	W	175	—	62	27
Swinesherd 3	886541	G	200	—	1	0
Swinesherd 4	886541	W	200	—	3	0
Swinesherd 5	886541	W	200	—	13	0
Swinesherd 6	877540	H	175	—	48	34
Tiddesley Wood	930444	W	100	+	11	4
Wadborough	913480	H	100	+	2	1
Whittington	878522	H	175	—	19	0
Worcester 1	868535	H	150	—	7	0
Worcester 2	868530	G	150	+	3	0
Worcester 3	866528	RH	100	+	9	0
Worcester 4	866528	RH	100	+	22	0
Worcester 5	869522	RH	125	—	23	0
Worcester 6	868539	H	100	+	1	0
Worcester 7	874541	H	200	—	33	0
Worcester 8	875540	RH	175	+	1	106
Worcester 9	866538	G	200	—	1	0
Worcester 10	865541	RH	225	—	36	0

Notes

1. Grid reference. Six-figure reference on the National Grid. All sites fall in the 100-km. square SO,

2. Habitat. W = Wood. H = Hedge. TH = Tall herbage. RH = Rough herbage. G = Grassland. For further explanation see text.

3. Altitude. In feet above mean sea-level; to the nearest 25 feet.

4. Water. + = Near water. — = Not near water. For further explanation see text.

5. Columns headed "*C. nemoralis*" and "*C. hortensis*" give the total numbers of each species found.

6. Remaining columns give the number of shells of each morph taken at each site, blank indicating none. 0 = Unbanded. 3 = Mid-banded. L = *Listeria* (00345). 5 = Five-banded and its minor modifications. UF = Shells with fusions involving the upper bands. LF = Shells with fusions involving the lower bands. FB = Banded, not hyalozonate. HY = Hyalozonate banded.

TABLE 1 (continued)

<i>C. nemoralis</i>												<i>C. hortensis</i>										
Yellow						Pink						Brown										
0	3	L	5	UF	LF	0	3	L	5	UF	LF	0	3	L	5	UF	LF	0	FB	HY	UF	LF
	1					2	2			1	1	1						1	1			
			1					1	2	3			3					7	9		6	6
								1	1	3	1	1						33	21	1	3	1
1	2					1	6	2	2	1	1		5					2	6		2	
		2		1	1				5	1	3		1					1				
									1	1	1							3	16		4	4
	2		11	8	8	6	11		23	9	10	6		1								
									10	4	5	2										
			1	1	1			1	3	11	9	1										
4		3	6	3	3	2	1	3	7	3	5	18		1								
	2		1	1		1	3		2		1	1						14	13		5	5
	6	1	11	3	2		2		4	3	3	2							1			
																		2	10		1	
																		19	25		5	8
	1	1	4	3	3			1	2	1	1											
	6		6	4	3			1	1	2	2	2										
	1							1		3	1	1	2									
1	1							1	1	6	4	5	1		1							
		1	1	1	2			3		16	5	4	7									
	1	3	5	3	2	4	4	2	4	2	2											
	1	1	3	1	1	2	11	3	9	7	10	1										
	2								3	2												
	6					1	9	2	1		2	5										
	3	2	9	3	3		1	3	4	2	1	3	1									
							1		1	1												
10		7	2	2		12	3	10	9	3	6	9	2					18	25	1	10	13
	1																	19	8		2	2
						3																
						7	2	1	2	2	2	1										
2	5	10		3	6	1	4	7	16	7	17	3										
	1				1	1	2	2	1			2	1		1			25	9		1	5
1																		2	2		1	
3		7	3	4															1			
1	1	3					6		3	2	3											
													1		1		1					
2		7	2																			
4		9	2			1	2	1	2			3										
1	1	13	1	1				2	5	1	1	1										
	1																					
5	11	8	1	4				1	5	2		2										
		1	1	1																		
								1														
1		5	2	2		9	6	13	4	10		2										

were taken from thrush-stones. Sheppard (1951) found that snails in a marked population were not carried to anvils that were only 30 m distant in woodland; A. J. Cain and J. D. Currey (pers. comm.) have found few snails in a marked population in open downland being carried as much as 50 m. Thus the collections gathered by thrushes probably originated from areas of approximately the same size as those within which I collected.

The snails were subsequently scored following the methods of Cain and

Sheppard (1950, 1954) and Cain and Currey (1963a). The scores for all collections are shown in table 1, omitting minor variants such as *punctata* (also called *interrupta* and *bandes pâles*) since these are not easy to score in some samples of old shells. For some sites, the figures result from a number of collections made at intervals during the 2-year study. Since in no case were repeated collections from the same site significantly different from each other, they have been lumped in table 1.

In this work only collections with more than four individuals of the species in question have been considered, except where otherwise stated. This lower limit is smaller than is usual in work on *Cepaea* simply because of the paucity of snails in the district.

The sites of collection have been grouped into five vegetational categories: woodland (mixed deciduous, usually with *Quercus* as the original, if not the dominant, species), hedgerows, tall herbage (patches of *Urtica*, *Epilobium*,

FIG. 1.—Distribution of sampling points in Worcestershire. Filled circles: woods. Crossed circles: hedgerows. Circles with two vertical lines: tall herbage. Circles with one vertical line: long grass. Circles with one horizontal line: rough herbage. Kilometre squares of the national grid are shown at the edges of the diagram.

etc.), rough herbage (long grass mixed with much broadleaved herbage), grassland (long grass mixed with very little broadleaved herbage: mostly unploughed corners of old leys or railway embankments). The classification of each site is given in table 1, together with the height above mean sea-level and whether or not it is within 100 m of a piece of water large enough to be shown on the 1:63360 Ordnance Survey map (a category including streams wider than about three-quarters of a metre). Both of these features would be expected to influence the micro-climates of the sites. The location and vegetation of each site is shown in fig. 1.

3. ECOLOGICAL RELATIONS OF THE TWO SPECIES

There is no evidence of broad geographical differences in the distribution of the two species of *Cepaea* in Worcestershire. Their relative frequency is not correlated with proximity to water. There are indications, though not statistically significant, that *C. nemoralis* is relatively commoner in woods and that the numbers of the two species in samples are inversely correlated.

C. nemoralis is relatively more frequent at higher altitudes (regression of arcsin transformed relative frequency on height a.s.l.: $P = 0.021$). This is reminiscent of the situation on the Marlborough Downs (Cain and Currey, 1963a), which is repeated in a less clear fashion on Salisbury Plain (Cain and Currey, 1963b): there, the valleys and bottoms of scarp-slopes have a preponderance of *C. hortensis* and the uplands have *C. nemoralis* only, the difference often being very clear-cut. Cain and Currey believed that *C. hortensis*, being the more northern species, was more able to withstand the ponding of cold air which occurs at night-time in the valleys and Cameron (1970a, b, c) has provided much physiological, behavioural, and ecological evidence that it is generally better adapted to cooler and damper conditions.

Only two other snails of similar size to *Cepaea* were found, *Helix aspersa* Mull. and *Arianta arbustorum* (L.). The former, considerably bigger than *Cepaea*, was found at several sites. *Arianta*, which is superficially much like *Cepaea*, was found only at Pershore, beside the river; it is known to be adapted to wetter habitats than *Cepaea* (Cameron, 1970a, b, c).

4. POLYMORPHISM AND BACKGROUND IN *C. nemoralis*

The vegetation categories from which *Cepaea* was collected fall into two types when considered from the point of view of the visual background they present. On the one hand, woods present a dark but relatively uniform background, composed of areas of leaf-litter. On the other hand, grassland, rough herbage, tall herbage, and hedgerows all present lighter but exceedingly broken backgrounds, composed largely of green or yellow leaves, stems, and grass-blades and the dark shadows between them. For no morphs studied here are there significant differences in frequency between open habitats of different types. There are, however, differences in morph-frequency between open habitats (lumped) and woods. Fig. 2 shows this for yellows and for effectively unbanded (*i.e.* shells with at least the upper two bands absent).

The trends for woods to have lower frequencies of yellow and higher frequencies of effectively unbanded than open habitats are highly significant ($P = 0.003$ and 0.002 ; U-test: Whitney and Mann, 1947). It would appear

FIG. 2.—Frequencies of yellow and effectively unbanded shells in samples of *C. nemoralis* from various habitats. Symbols as in fig. 1.

that yellow snails are relatively less successful in woods than in open habitats, whereas the reverse is true for snails which are effectively unbanded. Considering the nature of the visual backgrounds in woods and open habitats, this could be due to visual selection by predators favouring the more cryptic morphs. The hypothesis that the correlations with habitat are due to correlation of morph-frequency with other variables with which habitat is also correlated, is discussed below.

If visual selection were largely responsible for determining morph-frequencies in the region, one would expect any form of pigmentation which causes the shell to appear darker or less banded to be commoner in woods than in open habitats. In the following account such differences between habitats are examined: even those which are not statistically significant when considered in isolation are discussed, for their combined occurrence may well be significant.

Non-yellow shells may be pink or brown. On average, pinks are 1.5 times and browns 1.7 times commoner in woods than in open habitats ($P = 0.04$ and 0.3 : U-test).

In these collections the effectively unbanded condition is caused by three genetically dominant variants at three unlinked loci. In order of increasing

unbandedness and epistasis these are *listeria* (00345), mid-banded (00300), and unbanded. All are commoner in woods than in open habitats—*listeria* 1.3 times commoner, mid-banded 1.8 times, and unbanded 2.7 times ($P = 0.7, 0.002, 0.009$: U-test). Furthermore, it appears that, as one would expect if visual selection were largely responsible for governing morph-frequencies, the difference in frequency between habitats for any one morph is proportional to the number of bands missing in that morph. (Note: by *e.g.* "frequency of mid-banded" one means the frequency of mid-banded in the banded class, a similar convention being used in all cases of epistasis.)

Many of the banded snails show fusions of the bands. One might expect that fusions would be more common in woods than in open habitats, since such fusions would reduce the stripiness of the shell and also make it darker. This is true: both "upper fusions" (those involving the upper two bands) and "lower fusions" are 1.4 times commoner in woods ($P = 0.2$ and 0.3).

It will be shown below that absence of bands is much commoner in browns than in pinks, and in pinks than in yellows. Thus one ought to analyse the differences in frequency of unbanded between habitats taking one colour at a time rather than altogether. If this is done, one finds that unbandeds are commoner in woods than in open habitats in all colours, but that the trend is only significant in pinks (yellow, $P = 0.45$; pink $P = 0.0031$; brown, $P = 0.34$).

5. POLYMORPHISM AND BACKGROUND IN *C. hortensis*

The *C. hortensis* found during this study show a much smaller range of variation than the *C. nemoralis*. All except one brown (or perhaps pink) individual from Wadborough, are yellow. As usual, none is mid-banded or *listeria*. Two hyalozonates represent the only morph found in *C. hortensis* and not in *C. nemoralis*.

The mean frequency of unbandeds is almost identical in woods and open habitats. This is also true in the Oxford region, where the *C. hortensis* are also mainly yellow (Clarke, 1960). It seems as though the disadvantage which bands give in woods, by producing stripiness, is cancelled, or even outweighed, in yellow shells by the advantage they give by darkening the shell.

As in *C. nemoralis*, fusions are commoner in woods than in open habitats (upper fusions, 1.9 times commoner, $P = 0.003$; lower fusions, 2.1 times commoner, $P = 0.02$).

6. POLYMORPHISM AND FURTHER ENVIRONMENTAL VARIABLES

In neither species does the distribution of morphs show any geographical trends or correlation with proximity to water, but there are apparent correlations with altitude. Eight morphs (yellow, pink, brown, unbanded, mid-banded, *listeria*, upper fusions, and lower fusions) have been considered in this context in *C. nemoralis*. Since eight possible relations have been examined, I have adjusted the significance tests as Cooper (1969) recommended, taking 0.006 as the 0.05 level. On this criterion even the most pronounced relationship, a positive regression of frequency of *listeria* on altitude is not significant ($P = 0.01$).

The effect of altitude on the frequencies of unbandeds and both types

of fusions in *C. hortensis* has been examined, so that 0.017 is the significant probability level. Unbanded are commoner at higher altitudes (fig. 3; regression of arcsin transformed frequency = $15 + 0.25$ height a.s.l.: $P = 0.01$). In contrast, upper fusions are apparently commoner at lower altitudes. However, this correlation is spurious: woodland sites, which have more upper fusions, are generally lower than open sites and partial

FIG. 3.—Relation of frequency of unbanded shells in samples of *C. hortensis* to altitude. Symbols as in fig. 1.

regression analysis shows that, while the effect of habitat on frequency of upper fusions is significant ($P = 0.004$), that of altitude is not ($P = 0.4$).

7. MORPH FREQUENCIES IN MIXED COLLECTIONS

No correlations between the frequencies of the same or corresponding morphs in the two species are detectable. However, there are only five collections with five or more individuals of each species and it is thus impossible to detect any but the most marked correlations.

8. THE EFFECT OF ONE SPECIES ON THE POLYMORPHISM OF THE OTHER

In order to make an objective estimate of the level of polymorphism in a population, I have used a statistic which I call the Index of Polymorphism

and which is equal to $\left(1 - \sum_{i=1}^m p_i^2\right)$, where p_i is the frequency of the i th of the m morphs present. This index is equal to the chance of picking individuals of different morphs when one takes two individuals randomly from an infinite population. It is the complement of Simpson's (1949) "measure of concentration", to which Dr L. M. Cook kindly directed my attention. Simpson pointed out that an unbiased estimator of $\sum p_i^2$ is

$$\sum n_i(n_i - 1)/N(N - 1)$$

where n_i is the number of the i th morph in a sample and N is the sample size.

The Index of Polymorphism has a possible maximum of $\left(1 - \frac{1}{m}\right)$ and a possible minimum of zero. For *C. nemoralis* populations I recognise nine morphs only for the purpose of calculating the Index of Polymorphism, giving a possible maximum of 0.89. These are three banding patterns (unbanded, mid-banded plus *listeria*, and five-banded plus its minor modifications) in the three colour classes. To recognise more morphs would add little to the value of the statistic, for other morphs are usually rare and rare morphs

FIG. 4.—Relation of degree of polymorphism of *C. nemoralis* to frequency of *C. nemoralis* in total *Cepaea*. The maximum degree of polymorphism possible with the number of morphs present is indicated.

affect the value only slightly. In *C. hortensis* fusions of bands play an important part in the overall variation and so the three banding patterns recognised in calculating the Index of Polymorphism are effectively unbanded (usually comprising truly unbandeds and hyalozonate shells), banded without fusions involving the upper bands, and banded with such fusions. Fusions of upper bands rather than total fusions are considered since this makes discussion of the visual properties of the polymorphism more meaningful and, as far as one may guess, leads to an equally sound measure of genetic diversity.

Examination of the data for both species suggests that populations in woods and hedges may have rather higher Indices of Polymorphism than those from other habitats, but this trend is far from significant statistically. The most marked regular variation in the Index of Polymorphism is that *C. nemoralis* populations with which *C. hortensis* is also found almost invariably have rather high Indices of Polymorphism, whereas those from which the congener is absent may have high or low Indices of Polymorphism (fig. 4; $P = 0.002$, median test, Fisher's exact method). As fig. 5 shows, it is possible that a similar effect occurs in *C. hortensis*, but the data are too few for one to judge.

FIG. 5.—Relation of degree of polymorphism of *C. hortensis* to frequency of *C. hortensis* in total *Cepaea*. The maximum degree of polymorphism possible with the number of morphs present is indicated.

The frequencies of individual morphs of *C. nemoralis* are not apparently affected by the presence of *C. hortensis*. Thus the effect on the Index of Polymorphism seems to be one operating on the polymorphism as a whole, not an individual loci.

9. INTERACTIONS BETWEEN LOCI

None of the individual collections is large enough for linkage disequilibria, except of the most extreme kind, to be detectable within them. However, counting collections showing disequilibria in each direction, one finds more unbanded in pinks than in yellows (10 samples to two: $P < 0.025$), more in browns than in yellows (21 to one: $P < 0.001$), and more in brown than in pinks (24 to zero: $P < 0.001$). Thus yellows tend to be the most banded of the colour classes, brown the least. The tendency is manifest in all habitats.

The distribution of the various patterns of banding—mid-banded, *listeria*, fusions—is not markedly different amongst the three colour classes.

The reduced variation of *C. hortensis* makes the search for linkage disequilibria in this species impossible.

10. CONCLUSIONS

(i) *Visual selection*

The most obvious result obtained in this survey is that morph-frequencies in the regions appear to be largely governed by visual selection. It might be argued, as Lamotte (1959) has done, that the visual correlations obtained are, perhaps, spurious: that they are the result of some other selective difference between woods and open habitats. If, for instance, yellow snails are more resistant to strong sunlight, as Lamotte's experiments suggest, there might be a selective differential between woods and open habitats due to this; it would parallel that due to selective predation. Such parallel selective differentials may be responsible for the results obtained.

If visual selection is largely responsible for the determination of morph-frequencies in *C. nemoralis*, then one may expect to find certain differences between colonies in different habitats. They are:

1. Yellows will be more frequent in open habitats than in woods.
2. Pinks will be more frequent in woods.
3. Browns will be more frequent in woods.
4. Unbandeds will be more frequent in woods.
5. Mid-bandeds will be more frequent in woods.
6. The increase in frequency of mid-bandeds in woods will be less than the increase in frequency of unbandeds, since the single band reduces their effective unbandedness.
7. *Listeria* will be more frequent in woods.
8. The increase in frequency in *listeria* in woods will be less than that of mid-bandeds.
9. "Upper fusions" will be more frequent in woods.
10. "Lower fusions" will be more frequent in woods.
11. The increase in frequency of lower fusions in woods will be less than that in upper fusions, since they are less often exposed to view.

Of these predictions, the three concerning colour, being partially inter-dependent, should perhaps be regarded only as two. All the rest are independent, giving 10 separate predictions. It has been shown that all of them agree with the facts, except the last. Such agreement would be produced by chance only once in 102 times if the basis of prediction were incorrect (the fact that some of the predicted differences are not statistically significant is of no importance—it is the correctness of their direction which matters).

While the regularities in distribution of an individual morph may be explained by non-visual selection paralleling visual selection, that of 10 independent morphs is unlikely to be due to such chance parallels. Furthermore, whereas Lamotte (1959) has pointed out that one would expect an excess of yellows in open habitats as opposed to woods, since yellows are more resistant than the darker morphs to insolation and extreme temperatures, his experiment also showed that five-banded snails are less resistant than unbandeds to such extremes, so that one would expect to find bandeds in woods rather than open habitats. Thus the hypothesis that micro-climatic selection, rather than visual selection, is largely responsible for the determination of morph-frequencies in Worcestershire does not agree in its predictions with the facts.

It is more difficult to predict the differences between habitats one would expect in *C. hortensis*. As has been pointed out, one would not expect unbandeds and hyalozonates to be commoner in woods than in open habitats, so failure to find such a difference is not disturbing. One would, however, expect that upper fusions would be commoner in woods, that lower fusions would show a similar tendency, and that the tendency would be less marked for lower fusions than for upper fusions. The first two of these predictions are fulfilled, which suggests that morph-frequencies in *C. hortensis* may also be influenced by visual selection.

((i) *Altitudinal correlations*)

Two of the three apparent correlations between morph-frequency and altitude may not be real, but that between unbanded in *C. hortensis* and increasing altitude seems genuine. It is interesting that in two other areas of southern England the reverse correlation has been found (Cameron, 1969; Bantock and Noble, 1973). It has been suggested that yellow unbandeds are particularly resistant to night-time frosts, which are intense in valley bottoms in these two areas as in dune-land hollows, where yellow unbanded *C. hortensis* may also tend to be common (Cain, Cameron and Parkin, 1969). The topography of the Worcestershire area is quite different from that of these other areas, but it is nevertheless surprising to find the altitudinal correlation completely reversed.

((iii) *Polymorphism and the presence of a congener*)

The effect which *C. hortensis* appears to have on the polymorphism of *C. nemoralis* has several possible interpretations. It may be that the presence of *C. hortensis* indicates poor conditions for *C. nemoralis* and that heterosis is more marked in poor conditions, as seems to be general (Parsons, 1966). It may be that heterosis is more marked under competition from the

congener. It may be that the presence of *C. hortensis* indicates abundant environmental diversity, conducive to the survival of many morphs. It may be that the polymorphism of *Cepaea* involves systems of inversions, as in *Drosophila*, which, following the ideas of Carson (1955, 1958), are selected for in good environments where crossing-over would break up highly adapted gene combinations and are selected against in poor habitats where crossing-over would produce the necessary genetic diversity for dealing with environmental vicissitudes. Finally, apostatic selection (Clarke, 1962*a*, *b*; Greenwood, 1969; Elton and Greenwood, 1970) could explain the increased diversity in the presence of a similar species. While some of these possibilities may seem inherently more probable than others, there is no way at the moment to choose between them.

(iv) *Linkage disequilibria*

Linkage disequilibria between the colour and banding loci, especially the paucity of banded browns, are well known in *C. nemoralis* (Cain and Sheppard, 1950, 1954; Sheppard, 1952; Goodhart, 1956, 1958; Clarke and Murray, 1962; Cain and Currey, 1963*a*, *b*; Guerrucci-Henrion, 1966). The significance of these disequilibria has been discussed by Cain and Sheppard (1954) and Cain and Currey (1963*a*). The universal deficiency of banded browns was put down by the former to non-visual selection of constant direction. They found, however, that the disequilibria involving yellow and pink were not constant in direction: in the Oxford region, where visual selection seems the chief determinant of morph-frequencies, banding was in an excess in yellows in woodland and was deficient in that colour in open habitats. It was suggested that in woods banding was less disadvantageous in yellows than in pinks, due to the strong darkening effect of bands in yellows.

In Worcestershire the situation is different from that in the Oxford region, for there is a deficiency of unbanded yellows in all habitats, just as Cain and Currey (1963*b*) found in part of Salisbury Plain and Guerrucci-Henrion (1966) found in Brittany. It seems possible that in those three regions non-visual selection may be responsible for the disequilibria, as it almost certainly is on the Marlborough Downs, where the direction of the disequilibria shows "area effects" (Cain and Currey, 1963*a*).

(v) *General*

Visual selection is now well established as an effective force acting in populations of *C. nemoralis* and *C. hortensis* in several parts of central England (Cain and Sheppard, 1954; Currey, Arnold and Carter, 1964; this paper). Lamotte (1959), working on *C. nemoralis*, has discovered correlations with habitat in parts of France and also correlations of regional mean gene-frequencies with various climatic factors. Guerrucci-Henrion (1966) has found a correlation between distance from the coast and frequency of yellow in colonies in Brittany; one has suggested climatic factors which may be responsible for producing such correlations. Cain and Currey (1963*a*) presented evidence, both from geographical distribution over Europe and local distribution over the Marlborough Downs, that in *C. nemoralis* dark browns are associated with cool conditions. Despite the discovery of these

regularities in the distribution of various morphs, the French workers, especially, are disturbed by the wide variation of morph-frequencies shown by colonies from similar habitats and geographical positions. This study has shown, on the basis of a few small collections, that within even a small area of countryside both visual and non-visual selection may be operating effectively on populations of *Cepaea*. In a situation in which some character is affected by a number of variables, one expects a wide variation still to remain in the character even when one of the variables is stabilised. Thus the wide variation in gene-frequencies of *Cepaea* populations can be explained as the product of several selective forces, in combinations which are unique for each population. The occurrence of demonstrable regularities renders it unlikely that random genetic drift plays more than a minor role in the populations studied.

Acknowledgments.—It is a great pleasure to acknowledge the help and advice given to me during this work by my supervisor, Professor A. J. Cain. I would also like to thank Dr R. A. D. Cameron and an anonymous referee who made useful comments on an earlier draft of this paper and Professor Cain and R. Dennell for the facilities with which I have been provided in the Manchester University Department of Zoology.

During this work, I held the Philip Buckle Scholarship in Agricultural Zoology and a Science Research Council Studentship.

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