SELECTION IN MIXED COLONIES OF *CEPAEA* *NEMORALIS* AND *CEPAEA HORTENSIS*

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1. INTRODUCTION

Cain and Sheppard have shown (1954) that there is a correlation between the proportion of morphs in a population of *C. nemoralis* and the background of the habitat on which the snails occur. They have argued that this correlation is most likely to be due to selective visual predation, the most cryptic morph in any habitat being favoured. Clarke (1960) has found a comparable correlation in *C. hortensis*. As in *C. nemoralis* the most cryptic morph is at a high frequency but the crypsis is brought about in a different way, *i.e.* in woods (with dark uniform backgrounds) *C. nemoralis* has a high proportion of brown and pink unbanded morphs, whereas *C. hortensis* has a high proportion of banded yellows with fused bands, both species thus having a high proportion of effectively dark morphs.

Cain and Sheppard suggested that since the polymorphism was stable and old (Diver, 1940), there was some physiological advantage of the heterozygote maintaining it. However, since there were always rarer non-cryptic morphs present as well as cryptic ones, they considered the possibility of a frequency-dependent visual selective mechanism maintaining the polymorphism. In such a situation phenotypes would be at an advantage when rare. The kind of mechanism that might be acting is suggested by the works of Reighard (1908), De Ruiter (1953), and Tinbergen (1960) who showed that predators formed searching images for their prey. In the case of *Cepaea* the predator would form a searching image for the most common morph, which in the Oxford district would be the most cryptic. Thus the rarer non-cryptic morphs would be at an advantage. Cain and Sheppard could find no evidence that this was the case.

Clarke (1962a) in his analysis of Popham's data has shown, however, that frequency dependent visual selection can be effective in other species under some conditions. Later (1962b) he offered evidence that such frequency dependent visual selection, which he called apostatic selection, is important in determining morph frequencies in mixed colonies of *C. nemoralis* and *hortensis*. Lamotte (1951, 1959) has shown that there is no parallel variation in response to visual selection for crypsis in the two species, *e.g.* he found no significant correlation between the proportions of unbandeds in either species, but, as Clarke pointed out, the two species respond to visual selection in a similar way, but by different morphs. He therefore considered

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it more reasonable to compare the proportions of classes of morphs with visually similar properties.

One of the comparisons that Clarke made was between the proportions of yellow *nemoralis*, and yellow effectively unbanded *hortensis*. This showed a significant overall positive correlation, *e.g.* the samples from woods contained a higher proportion of effectively dark shells than did the samples from open habitats. There was however, a significant negative correlation of yellow *nemoralis* and yellow effectively unbanded *hortensis* in samples taken from open habitats. Thus he suggested that visual selection for crypsis is important in both species but apostatic selection is also operating, the rarer species obtaining an advantage by being distinct from the more common one.

During the past three years I have collected samples from mixed colonies in a survey of both species on the Berkshire Downs. Using the methods of analysis given by Clarke (1962*b*) I have obtained results that conflict with his conclusions. These results are presented here with a discussion of Clarke's data and conclusions.

2. METHODS

(i) Collecting

Random samples were collected from mixed colonies of *C. nemoralis* and *C. hortensis* and, in certain cases from unmixed colonies nearby for comparison. All the samples come from the Berkshire Downs. Data from previous workers' samples taken from the Berkshire Downs (Clarke, 1962*b*, and unpublished), Salisbury Plain (Cain and Currey, 1963*b*) and from the Oxford district (Clarke, 1960, 1962*b*) have also been used.

(ii) Scoring and classes of morphs considered

Shells were scored for age, condition (live, dead, whole or predated), colour and banding (Cain and Sheppard, 1954; Cain and Currey, 1963; Clarke, 1960). Juveniles were not included in the score of a sample as it was not possible to tell which species they were. Samples with less than ten individuals of either species were not included in the analysis. The classes of morphs considered were those given by Clarke (1962*b*) and are shown in table 1.

(iii) Statistical tests

The main test used was that given by Clarke (1962*b*).

3. RESULTS

(i) Distribution of mixed colonies of *C. nemoralis* and *C. hortensis* on the Berkshire Downs

C. nemoralis and *C. hortensis* occur widely over the Berkshire Downs (Carter, in preparation), although *C. hortensis* occurs only sporadically in the east, mostly in the dry valleys of the Chalk plateau. In the west this species is very common on the face of the escarpment to the

TABLE 1
The composition of random samples of Cepaea nemoralis and Cepaea hortensis with regard to certain classes of morph found in mixed colonies on the Berkshire Downs, the Oxford district and the Chilterns

Map reference	<i>C. nemoralis</i>				<i>C. hortensis</i>			
	Sample size	Yellow	Yellow effectively unbanded	Effectively yellow	Sample size	Yellow effectively unbanded	Effectively yellow	Habitat
<i>The Berkshire Downs—Goring District</i>								
SU 459829	21	14	1	12	44	15	33	Hedgerow
SU 467831	62	19	19	19	59	34	52	Long grass
SU 490812	10	3	0	2	50	2	34	Mixed deciduous wood
SU 402792	102	31	0	21	23	4	19	Beech wood
SU 482821	45	11	10	10	28	10	24	Long grass
SU 545810	17	2	0	2	10	0	8	Hedgerow
SU 568822	25	0	0	0	40	17	31	Beech wood
SU 556837	66	12	3	8	57	10	24	Beech wood
SU 567817	120	12	5	10	18	5	7	Beech wood
<i>Lambourn District</i>								
SU 326862	88	81	8	38	128	3	58	Rough herbage
SU 335858	101	101	59	82	20	14	14	Long grass
SU 355858	87	87	77	77	317	206	276	Rough herbage
SU 358859	18	18	13	13	162	45	95	Rough herbage
SU 359860	19	19	19	19	38	21	33	Rough herbage
SU 360861	9	8	8	8	159	82	115	Rough herbage
SU 362861	13	12	12	12	36	17	29	Long grass
SU 365854	13	13	8	9	45	15	38	Rough herbage
SU 368873	40	23	21	23	21	18	20	Rough herbage
SU 374844	127	87	39	47	12	2	6	Long grass

TABLE 1—continued

Map reference	<i>C. nemoralis</i>				<i>C. hortensis</i>			
	Sample size	Yellow	Yellow effectively unbanded	Effectively yellow	Sample size	Yellow effectively unbanded	Effectively yellow	Habitat
<i>Lambourn District—contd.</i>								
SU 395776	20	0	0	0	29	0	28	Long grass
SU 339810	160	89	72	73	36	3	20	Beech wood
SU 332822	12	5	4	5	156	14	117	Beech wood
SU 354857	26	26	20	21	83	61	68	Rough herbage
<i>Uffington District</i>								
SU 286857	60	28	0	15	109	56	96	Long grass
SU 289858	67	65	3	52	77	11	76	Rough herbage
SU 293847	41	7	4	7	34	23	26	Beech wood
SU 296850	34	26	16	18	29	2	19	Long grass
SU 297849	28	23	19	21	44	3	34	Long grass
SU 297865	145	98	55	60	43	0	37	Short turf
SU 299866	96	67	36	37	47	0	28	Short turf
SU 301868	106	35	19	20	20	18	20	Long grass
SU 302870	32	7	2	4	27	13	22	Rough herbage
SU 303777	103	69	22	52	134	54	88	Rough herbage
SU 307804	14	13	7	7	64	24	41	Rough herbage
SU 308869	22	11	3	6	15	7	13	Mixed deciduous wood
SU 311865	143	123	63	76	20	3	11	Beech wood
SU 274857	14	5	1	5	34	0	14	Long grass
SU 275856	11	8	0	4	88	6	68	Long grass

TABLE 1—continued

Map reference	<i>C. nemoralis</i>				<i>C. hortensis</i>			
	Sample size	Yellow	Yellow effectively unbanded	Effectively yellow	Sample size	Yellow effectively unbanded	Effectively yellow	Habitat
<i>Liddington District</i>								
SU 221801	16	12	1	3	93	52	91	Rough herbage
SU 222807	29	26	3	12	149	27	146	Rough herbage
SU 223795	63	44	0	33	175	67	154	Rough herbage
SU 223796	58	42	0	36	118	42	95	Rough herbage
SU 223796	93	80	1	48	122	33	97	Rough herbage
SU 239827	22	3	2	3	43	24	35	Rough herbage
SU 240826	26	2	1	2	31	12	30	Long grass
SU 242774	21	17	0	8	77	35	57	Rough herbage
SU 234783	41	25	0	19	21	15	19	Rough herbage
SU 244799	14	4	0	4	77	22	52	Rough herbage
SU 248797	11	1	0	1	16	4	13	Rough herbage
SU 264789	18	14	0	14	54	28	54	Nettles in grass
SU 245822	36	8	1	3	28	10	22	Rough herbage
SU 258819	16	9	0	6	127	64	115	Rough herbage
SU 244829	38	12	1	1	19	0	6	Rough herbage
SU 249824	18	7	1	3	13	1	13	Rough herbage
SU 246828	31	6	3	6	78	24	49	Rough herbage
SU 243821	84	31	3	14	15	1	13	Long grass
<i>The Oxford District and Chilterns (Clarke's Data)</i>								
SP 963150	23	1	0	0	90	4	32	Beech wood
SP 628131	51	0	0	0	72	20	34	Mixed deciduous wood

TABLE 1—continued

Map reference	<i>C. nemoralis</i>				<i>C. hortensis</i>			
	Sample size	Yellow	Yellow effectively unbanded	Effectively yellow	Sample size	Yellow effectively unbanded	Effectively yellow	Habitat
<i>The Oxford District and Chilterns (Clarke's Data)—contd.</i>								
SP 463010	104	11	2	9	180	28	80	Mixed deciduous wood
SP 551107	11	1	0	0	45	18	20	Mixed deciduous wood
SP 556096	45	11	4	9	62	28	42	Fen
SP 468012	13	5	3	4	36	13	26	Hedgerow
ST 844752	75	2	2	2	41	8	25	Beech wood
SU 747864	14	1	1	1	9	1	6	Beech wood
SU 718880	12	0	0	0	10	0	3	Beech wood
SU 743974	30	0	0	0	14	3	5	Beech wood
SU 469978	164	62	7	50	79	40	65	Fen
SU 346951	29	17	16	17	12	4	11	Hedgerow
SU 335936	15	5	0	0	58	14	32	Hedgerow
SU 317971	71	27	8	20	183	84	162	Hedgerow
SU 255911	8	4	1	2	16	12	16	Hedgerow
SU 469978	42	16	2	13	158	59	124	Fen
SU 463997	10	5	2	5	19	5	13	Fen
<i>The Berkshire Downs (Clarke's Data)</i>								
SU 180799	25	14	4	13	291	127	247	Nettles
SU 222808	69	51	16	31	227	53	220	Rough herbage
SU 219807	32	30	8	20	19	0	19	Short turf
SU 225824	21	11	1	10	15	11	14	Short turf
SU 243822	25	8	6	8	19	7	17	Rough herbage

TABLE 1—continued

Map reference	<i>C. nemoralis</i>				<i>C. hortensis</i>			
	Sample size	Yellow	Yellow effectively unbanded	Effectively yellow	Sample size	Yellow effectively unbanded	Effectively yellow	Habitat
<i>The Berkshire Downs (Clarke's Data)—contd.</i>								
SU 244798	30	2	0	1	57	31	56	Rough herbage
SU 269849	15	6	4	5	29	1	21	Beech wood
SU 296861	47	29	15	25	116	1	94	Short turf
SU 298869	36	17	15	15	17	3	16	Short turf
SU 301867	43	24	16	18	106	4	80	Short turf
SU 301867	13	11	2	4	39	0	37	Short turf
SU 301869	21	5	3	3	143	116	126	Short turf
SU 308868	22	22	10	11	26	1	24	Nettles in grass
SU 301869	17	5	2	2	77	32	49	Short turf
SU 304868	11	0	0	0	21	5	17	Mixed deciduous wood
SU 332858	15	15	10	13	214	96	158	Rough herbage
SU 333858	28	28	18	26	45	26	29	Rough herbage
SU 333858	75	75	47	66	187	120	146	Short turf
SU 335858	35	35	16	31	19	14	17	Rough herbage
<i>The Chilterns</i>								
SU 744984	63	6	0	3	59	20	47	Rough herbage

north of the Chalk plateau. *C. nemoralis* occurs commonly over the high plateau. Mixed colonies of the two species occur in both woods and open habitats in the east of the region, but mostly in the open habitats in the west. The morph frequencies differ in both species in the different districts on the Berkshire Downs that I have defined (Carter, in preparation), but the limits of the districts are similar in both species.

Clarke (1962*b*) considered the situation in which visual selection for crypsis and visual apostatic selection were acting together. This situation might be true of the eastern districts of the Berkshire Downs where visual selection for crypsis is effective, but in the western districts, visual selection for crypsis is most ineffective and in each district there are area effects for different morphs in the two species. As visual predation is occurring in these latter districts it is possible that apostatic selection is effective in some or all of them. In this case it could, in the absence of selection for crypsis, produce quite different results with regard to the type of morph selected for from those it might effect in districts where the two selective forces interact. I have therefore analysed the results of samples from mixed colonies taken from the different districts separately. The districts are from east to west; Goring, Lambourn, Uffington and Liddington. I have only a few samples from the Goring district with sufficient numbers to allow me to do a detailed analysis of morph frequencies and therefore I shall consider them after I have discussed the results from other districts.

(ii) *The Lambourn district*

Cain and Currey (1963*a*) have shown that there is an area effect in *C. nemoralis* in this district although visual selection for crypsis is partially effective in woods in the south. The samples from these woods have a higher proportion of pink morphs than do adjacent open habitat samples but there are no differences in the frequencies of the effectively unbanded morphs which are at a high frequency in all habitats. I have confirmed these results (Carter, in preparation) and have shown that the area effect is extensive although visual selection is partially effective over the whole district for morphs not taking part in the area effect. There is a very wide scatter of morph frequencies in *C. hortensis*, but a comparison of the two southern wood samples with adjacent open habitat ones shows no morph frequency changes that would agree with the hypothesis of visual selection for crypsis. The open habitats are half a mile away from the woods, which is too great a distance for their similarity in morph frequencies to be explained by gene flow. There is no evidence of variation of morph frequency with habitat in the samples of this species taken from the main part of the district.

A comparison of the frequency of yellow *C. nemoralis* and yellow effectively unbanded *C. hortensis* in mixed colony samples shows a slight positive correlation if all such samples are included in the

analysis ($P < 0.05 > 0.02$). This might be taken as evidence for visual selection for crypsis but the few samples from woods are from the south and should really be excluded from the analysis, as the selection pressures are probably rather different there from those in the main part of the district. If these and the nearby open habitat samples

FIG. 1.—A diagram showing the frequency of the unbanded and hyalozonate morphs of *C. nemoralis* and yellow midbanded and five-banded morphs of *C. hortensis* in the samples of mixed and unmixed colonies of the two species. Samples taken over a half-mile transect of Sparsholt Down in the Lambourn district of the Berkshire Downs.

are removed, the overall correlation is not significant $P < 0.05$. There is no negative correlation within the group of samples from open habitats such as was found by Clarke in a similar analysis (1962*b*). Analyses of the data using the other methods given by Clarke (1962*b*) give similar results to the above. There is therefore no evidence of apostatic selection in this district.

Fig. 1 shows a series of samples from mixed and unmixed colonies over a half a mile transect on Sparsholt Down. The lower series of histograms shows the proportions of unbanded and of hyalozonate morphs in *C. hortensis* and the upper series the proportions of yellow and midbanded morphs in *C. nemoralis*. The hyalozonate and unbanded morphs in *hortensis* are visually similar. On the hypothesis of visual apostatic selection one might expect that the combined frequencies of these two morphs would affect or be affected by the frequency of visually similar morphs of *C. nemoralis* in mixed colonies of the two species. Fig. 1 shows that there is no marked difference in the frequency of visually similar morphs between mixed and unmixed colonies in either species. This would argue against visual apostatic selection. It is also interesting that whereas the frequency of all the *C. nemoralis* morphs remains more or less constant, the unbanded and hyalozonate morphs in *C. hortensis* shows progressive and opposite changes with distance, indicating that selection is acting independently on the two species.

(iii) The Uffington district

A comparison of the frequency of yellow *C. nemoralis* and yellow effectively unbanded *C. hortensis* in mixed colony samples seems to suggest that apostatic selection is effective in this district, since there is a significant negative correlation within the group of samples from the open habitats ($P < 0.01$). There is also a significant negative correlation between the proportion of yellow effectively unbandeds in both species ($P < 0.05 > 0.02$). There is no evidence that visual selection for crypsis is effective on either species. These results are different from those found by Clarke (1962*b*) and it is possible that apostatic selection is operating here in the absence of visual selection for crypsis. There is however some evidence that it is not. Most of the samples from mixed colonies have been taken from the Chalk escarpment. *C. hortensis* is common at the bottom of the slope but extends up it. *C. nemoralis* on the other hand is common on the high plateau, and although it is found on the escarpment it is rare at the bottom. There are area effects in both species in this district, but in mixed colonies the characteristic morph frequencies of the area effects seem to break down. Fig. 2 shows the frequency of the yellow unbanded morph in *C. hortensis* in samples taken from mixed colonies on the escarpment at Uffington. These are the only effectively unbanded morphs present in these samples. The unbanded morph frequency is higher in the samples from the bottom of the slope than

FIG. 2.—A diagram showing the frequency of yellow unbanded morphs in samples of *C. hortensis*. Data from samples of mixed colonies on a transect up the escarpment at Uffington.

in those at the top. The morph frequency increases from the bottom of the slope then falls off rapidly, the morph being absent in the top five samples. Comparison of the frequencies of the various *C. nemoralis* morphs shows that the samples that have the highest frequency of dark colour morphs (browns and pinks) are those in which the proportion of yellow unbanded *C. hortensis* is highest, and also, where there is a high frequency of yellow effectively unbanded *C. nemoralis* the frequency of yellow unbanded *C. hortensis* is lowest. These results support the hypothesis that apostatic selection is effective, but fig. 3 shows the frequency of yellow unbanded *C. hortensis* in samples taken from *unmixed* colonies at Woolstone, half a mile west of Uffington. The changes in the proportion of the yellow unbanded morph are very similar to those in the mixed colonies at Uffington, although the morph does not reach such high frequencies as it does there.

Unfortunately I have not been able to obtain a parallel series of samples from unmixed colonies of *C. nemoralis*. There are three samples from apparently unmixed colonies at Uffington which have very similar morph frequencies to the nearby mixed colonies, but this could be due to gene flow since the colonies are less than 100 m. apart and the size of the panmictic unit has been shown to be approximately 60 m. (Lamotte, 1951; Murray, 1963).

The two series at Uffington and Woolstone are half a mile apart. This is much too great a distance to allow gene flow to cause any similarity of morph frequencies. It seems likely that there is some selective pressure bringing about a change in the frequency of unbanded *C. hortensis* regardless of the occurrence of *C. nemoralis*. It is possible that the *C. nemoralis* morph frequencies are determined apostatically, *i.e.* where *C. hortensis* is common, at the bottom of the slope, the rarer *C. nemoralis*'s morph frequencies may be determined by apostatic selection. Where *C. hortensis* is rare at the top of the escarpment the morph frequencies of *C. nemoralis* are determined by some selective factor causing area effects. There are, however, regular changes in the frequencies of brown *C. nemoralis* up the escarpment at Uffington and in other series of samples some distance away, so that it is possible that the changes in morph frequency of this species are not due to apostasis.

(iv) *The Liddington district*

In the comparison of the frequencies of yellow *C. nemoralis* and yellow effectively unbanded *C. hortensis* it was found that samples taken from the east and west of this district were heterogeneous. The samples were separated into two groups on their geographical position. Those from the east showed a random scatter in the above comparison, but the open habitat samples from the west showed a negative correlation ($P < 0.05 > 0.02$). No correlation with any environmental variable could be found that might account for this negative relationship. There is no heterogeneity in the comparison of the frequency of yellow

FIG. 3.—A diagram showing the frequency of yellow unbanded morphs in samples of *C. hortensis*. Data from samples of unmixed colonies on a transect up the escarpment at Woolstone, half a mile to the west of Uffington.

effectively unbanded morphs in the two species. This group of morphs is at a low frequency in *C. nemoralis* over the whole district. There is no significant correlation within the open habitat class in this comparison ($P > 0.05$). There are no overall positive correlations when samples from both woods and open habitats are included in either of the above analyses and therefore there is no evidence that visual selection for crypsis is effective. The evidence in favour of apostasis is conflicting, but it is possible that it is acting in the west.

(v) Salisbury Plain

Cain and Currey (1963*b*) collected samples of both species from part of Salisbury Plain and they have shown that there is no evidence that visual selection is effective in either species. They sampled several mixed colonies and pointed out that as there was no evidence for visual selection for crypsis they would not expect apostatic selection to be effective, nor could they find any evidence that it was. A comparison of the frequencies of yellow *C. nemoralis* and yellow effectively unbanded *C. hortensis* gives no evidence of any correlation. The proportion of yellow effectively unbanded *C. hortensis* is low in all samples regardless of the frequency of yellow *C. nemoralis*.

(vi) Comparison of morph frequencies in mixed and adjacent unmixed colonies of the two species

Some of the changes in the frequency of the light morphs of *C. nemoralis* and *C. hortensis* between mixed and nearby unmixed colonies can be used to investigate apostasis. In general, if the frequencies of a given class of morphs in each species are more dissimilar in mixed colonies than they are between adjacent unmixed colonies, this is evidence in favour of apostasis.

The method of comparison is as follows (fig. 4). The proportions of yellow *nemoralis* and yellow effectively unbanded *hortensis* are plotted along the abscissa and ordinate. The co-ordinates of greatest similarity of these two frequencies fall along the diagonal joining the two sets of co-ordinates (0 per cent., 0 per cent.) and (100 per cent., 100 per cent.). Lines drawn parallel to this diagonal represent equal degrees of similarity along their length, but the further they are away from the main diagonal, the more the degree of similarity that they represent decreases. The morph frequencies in the two unmixed colonies adjacent to each mixed colony are treated as if coming from a mixed colony (open circles in fig. 4). The mixed colonies are plotted as filled-in circles and each one is joined to its respective open circle representing the combined unmixed colonies. The morph frequencies in the mixed colony are more or less alike than those in the adjacent unmixed colonies depending on whether the filled-in circle is nearer to, or further away from the main diagonal than the open circle.

There are 18 samples from mixed colonies on the Berkshire Downs with sufficient numbers of shells and with unmixed colonies near

enough to carry out such an analysis. The distance between the colonies to be compared is never less than 200 yards or more than 800 yards. In 12 of the 18 comparisons the yellow *C. nemoralis* and yellow effectively unbanded *C. hortensis* frequencies are more alike in

FIG. 4.—A scatter diagram comparing the proportions of yellow “effectively unbanded” shells in *C. hortensis* and yellow shells in *C. nemoralis* in samples taken from mixed and unmixed colonies on the Berkshire Downs. Mixed colonies are represented by filled-in circles and unmixed colonies by open circles. Adjacent mixed and unmixed colonies are joined.

the mixed than in the unmixed colonies. In five mixed colonies the frequencies are less alike, and in one comparison the frequencies are the same in the mixed and unmixed samples. In the absence of apostatic selection or any other interaction between the two species, there should be equal numbers of mixed colonies which are more alike and less alike than their respective unmixed colonies. The result obtained is not significantly different from this expectation $\chi^2_{(1)} = 2.65$, $P > 0.1$.

4. DISCUSSION

Clarke (1962*b*) argued from his data that visual selection for crypsis and apostasis were interacting. However, some of his samples were

taken from the Uffington and Liddington districts. The results of the work presented here show that visual selection for crypsis is not effective in either of these districts, and therefore samples taken from them should not be included in any analysis of the interaction of the two forms of selection. Clarke, as he did not know of the occurrence of area effects, also collected samples widely both on and off the chalk in his (1960) demonstration of morph frequency variation with habitat in *C. hortensis*. Detailed surveys of snail populations on the chalk (Cain and Currey, 1963*a* and *b*; Arnold, in preparation; Carter, in preparation) have shown that visual selection is ineffective over most of such regions investigated. Isolated samples from different chalk regions should not, therefore, be considered together, in any analysis of the effects of visual selection. It is known that visual selection for crypsis is effective in *C. nemoralis* in the Oxford district (Cain and Sheppard, 1954) and along the northern edge of the Chilterns (Arnold, in preparation). Fortunately Clarke (1960) also sampled these districts

FIG. 5.—A scatter diagram for *C. hortensis* showing the relation between the percentage of "yellow effectively unbanded" shells, the percentage of banded shells with fused bands and the nature of the habitat. The data are from samples collected by Clarke (1960) in the vicinity of Oxford. Samples from woods, black circles; samples from fens, half black circles; samples from open habitats, open circles.

in detail for *C. hortensis*, although he combined the results with the others that he obtained. Since it is possible that his data was heterogeneous I have reanalysed those for the Oxford district and Chilterns alone.

Fig. 5 (Clarke's data) shows the proportion of yellow effectively unbanded morphs plotted against the proportion of banded morphs with some bands fused in *C. hortensis*. The ordinate is slightly different from that given by Clarke (1960) since I have included all those yellow morphs that are effectively unbanded, *i.e.* unbanded, hyalozonates and five-bandeds with the upper two bands missing, while Clarke used only yellow unbandeds. Clarke independently came to the conclusion that these morphs could be grouped in his 1962*b* paper. There is a separation between the samples from the darker and more uniform habitats (woods and ivy) and the lighter and more heterogeneous habitats (hedgerows and rough herbage). This separation is significant on both axes ($P < 0.02 > 0.01$ in both cases). Since the measurements along both axes are independent the χ^2 s can be summed. This gives a significant separation between the two groups of habitats with $P = 0.01$.

Inspection of Clarke's data (1960) shows that those samples which contain a low proportion of banded morphs with fusions have relatively high proportions of pinks and/or brown morphs. Since the proportion of banded morphs with fusions is being used as a measure of the proportion of effectively dark shells (Clarke, 1960), it is reasonable to include both pinks and browns with the yellow five-banded-fused. This does decrease the independence of the measurement of the effectively dark morphs from that of the yellow effectively unbandeds but the measurements are not the inverse of each other since the yellow five-banded-unfused are not included in the calculation of either proportion. Fig. 6 shows that using this method there is a very clear separation of the samples from the darker and lighter habitats. Both the woodland and more open habitat samples form closer groups than in fig. 5. If a line is drawn dividing the samples into two equal-sized groups, at right angles to the slope of the scatter, and the separation between the woodland samples falling below the line and the open habitat samples falling above the line is tested it is found to be significant with $P < 0.001$. Thus although several of the more open-habitat samples may contain a high proportion of five-banded morphs with fusions out of all the five-bandeds, the proportion of the five-bandeds in each sample as a whole is small, and therefore the darkening effect is not very great. In woods, however, the proportion of the five-bandeds is higher and consequently if most of these show fusion of bands the proportion of effectively dark morphs is high. In those woodland samples with a low frequency of yellows, the darkening effect is brought about by pinks and browns, most of which are unbanded, as well as by the fusion of bands in the yellows.

Clarke's data indicates that visual selection for crypsis is effective

in *C. hortensis* in the Oxford district and the Chilterns as he claimed, but the effectiveness is better shown by grouping morphs as in fig. 6 of the present paper. It is also clear from his data (1960) and my own (Carter, in preparation) that the species is more polymorphic for colour in these districts and other lowland districts in the south of England than on the high Chalk downland in Central England that has so far been investigated.

FIG. 6.—A scatter diagram for *C. hortensis* showing the relation between the percentage of yellow "effectively unbanded" shells and "effectively dark" shells. Data from samples collected by Clarke (1960) in the vicinity of Oxford. Symbols as in fig. 5.

Since visual selection for crypsis is effective in both species in the Oxford district and the Chilterns, Clarke's data from mixed colonies from these two districts can be considered together. (I have tested for heterogeneity between samples from the two districts, and there is none.) Fig. 7 makes a comparison between the proportion of yellow *C. nemoralis* and yellow effectively unbanded *C. hortensis* from Clarke's data and is therefore his fig. 4 (1962*b*) with samples taken from the Chalk removed. Fig. 8 shows the samples in fig. 7 plus a few that I have obtained from the Goring district of the Berkshire Downs. I

FIG. 7.—A scatter diagram showing the relation between the percentage of yellow “effectively unbanded” shells in *C. hortensis* and the percentage of yellow shells in *C. nemoralis*. Data from samples of mixed colonies in the vicinity of Oxford (Clarke, 1962). Symbols as in fig. 5.

have shown previously (Carter, 1965*a*) that visual selection for crypsis is effective in both species in this district, and have therefore felt justified, since the samples show the same trends, in lumping them with Clarke's.

It is evident in both figures that there is an overall positive correlation of the samples. In fig. 8 this is significant with $P < 0.001$. There is a separation between samples from woods and those from more open habitats on both axes ($P < 0.01$ in both cases). Since the measurements along each axis are independent of each other the χ^2 s can be summed giving a probability of $P < 0.001$. These results confirm that visual selection for crypsis is effective on both species in mixed colonies in these three districts.

There is no heterogeneity of the samples from different districts within the open habitat class in figs. 7 and 8 and thus these samples can be tested for a within-class correlation. With the test given by Clarke (1962*b*) there is found to be a non-significant positive correla-

tion ($r = 0.136$, $P > 0.1$) between the frequency of yellow *C. nemoralis* and yellow effectively unbanded *C. hortensis*. This is a quite different result from that obtained by Clarke who found that there was a significant negative correlation for the data from his samples, which included both those in fig. 7 and his samples from Liddington and Uffington, and other districts on the Chalk (his fig. 4).

FIG. 8.—A scatter diagram showing the relation between the percentage of yellow “effectively unbanded” shells in *C. hortensis* and the percentage of yellow shells in *C. nemoralis*. Data from samples of mixed colonies in the vicinity of Oxford (Clarke, 1962) and a few samples of mixed colonies from the Goring district of the Berkshire Downs. Symbols as in fig. 5.

A similar test on the samples from woods in fig. 8 gives a non-significant negative correlation ($r = -0.11$, $P > 0.1$) as was found by Clarke (1962*b*).

Fig. 9 gives a comparison of the effectively yellow morphs in both species from the three districts where visual selection is effective. There is a significant separation between the samples from woods and more open habitats ($P < 0.01$ on both axes), and there is an overall positive correlation by the medial test ($P < 0.05$). A similar positive correlation was found by Clarke (1962*b*) who therefore suggested that

although apostatic selection was effective within habitat classes (from his fig. 4) there was overall selection in mixed colonies for crypsis. The positive correlation is the only one that I have obtained in all similar tests for four sets of data and confirms that it is only in the Oxford district, the Chilterns and the Goring district that visual selection for crypsis is effective in both species in mixed colonies.

FIG. 9.—A scatter diagram showing the relation between "effectively yellow" shells in *C. hortensis* and *C. nemoralis*. Data from samples shown in fig. 13. Symbols as in fig. 5.

5. CONCLUSIONS

It is clear that the data collected by Clarke which he used in support of his hypothesis of apostatic selection are heterogeneous. He did consider this possibility (1962*b*) but, because it was not known at that time that area effects occurred extensively on chalk downland, he suggested that any such heterogeneity was unlikely. He did, however, point out that his evidence was not conclusive.

It is the collections from Chalk downland at Uffington and Liddington, in particular those from the open habitats in these districts, that are the main contributions to the negative correlation that he

obtained. Visual selection for crypsis is ineffective in these districts and the evidence for apostatic selection is questionable. Over two other districts on the Chalk there is no evidence for either apostatic or cryptic selection and therefore only the three districts where visual selection for crypsis is effective remain to be considered in the investigation of the interaction of visual selection for apostasis and crypsis. The data presented above concerning these three districts does not give any significant evidence of an interaction between *C. nemoralis* and *C. hortensis* which would support the hypothesis of apostatic selection. Although there is no significant positive correlation within each habitat class, which might be expected if both species were responding to visual selection for crypsis, there are several factors mitigating against finding such a correlation. The samples have been taken from three districts, which, although adjacent, cover a large area, and it is to be expected that selective pressures other than visual selection will differ in many of the colonies. Thus there will be a more or less broad scatter of morph frequencies even within similar habitats. There must also be considerable variation of the background within habitat classes (Cain and Currey, 1963a).

The separation between the samples from woods and those from the more open habitats and the overall positive correlation between samples, in the above three districts, do support the hypothesis that visual selection is favouring the most cryptic morphs in both species in any habitat. In those districts where visual selection for crypsis is ineffective the evidence is inconclusive, but it seems likely that there is some non-visual selective pressure determining morph frequencies independently in both species. It therefore follows that the hypothesis of apostatic selection in *Cepaea* has yet to be substantiated.

6. SUMMARY

1. In order to investigate whether apostatic selection and visual selection for crypsis interact (Clarke, 1962b), districts in which visual selection for crypsis occurs should be considered separately from those where it is ineffective or only partly effective.

2. Analysis of three districts in which visual selection for crypsis is effective in both species, and in which there are mixed colonies, gives no significant evidence of apostatic selection. The most cryptic morph in either species is favoured in any given habitat.

3. Analysis of four districts where visual selection is ineffective, or only partly effective, although visual predation does occur, gives no concrete evidence in favour of apostatic selection in *Cepaea*.

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