

SELECTION IN THE POLYMORPHIC LAND SNAIL
CEPÆA NEMORALIS

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INTRODUCTION

THE structure of natural populations of animals and plants and of variation both within and between colonies needs more study as Diver (1940) has pointed out. Research along these lines is of particular importance because of the evidence he has obtained that many, apparently continuous, natural populations are broken up into small breeding-communities, giving the conditions in which genetic drift, as suggested by Sewall Wright (*e.g.* 1940), might be expected to occur if it were operative. Diver has stated that from his observations on populations of *Cepæa nemoralis* (L.) and *C. hortensis* (Müll.) he obtained no indications that the variations in shell colour and banding have any selective value. He considers that these small breeding-communities show definite divergences from each other because of non-random mating, but expresses surprise (1940, p. 312) that such divergences have not proceeded further by means of genetical drift.

The purpose of this paper is to describe an investigation into this problem of the relative importance of selection and drift in determining the distribution of different colour and banding patterns in *C. nemoralis*. We find, on the contrary, that they have definite selective values, related to the environment, determining the general aspect of different populations and therefore of their gene ratios. Although small inbreeding communities within each population may diverge from one another in colour and banding patterns, this random divergence cannot proceed far, because of the effects of natural selection.

METHODS

(i) *Collecting*

Collections were taken from various localities in southern England, situated, with one exception, within a fifty-mile radius of Oxford,

chiefly to the south and west. The localities were chosen for diversity of vegetation, and when possible several widely separated colonies on the same type of vegetational background were examined. Fig. 1 is a sketch-map showing the localities. The dryness of the summer (1949) has made the collection of large samples very difficult, as the animals have remained buried for long periods.

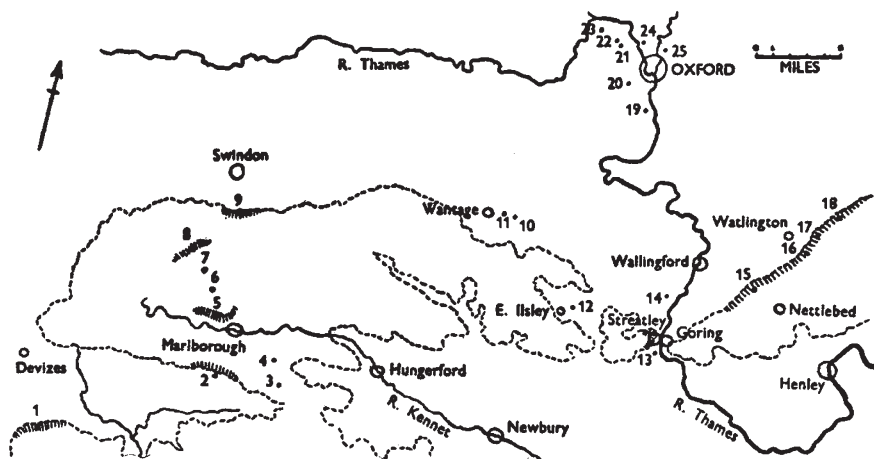


FIG. 1.—Sketch map showing the collecting localities. The broken line represents the 500-foot contour. Steep chalk scarps from which collections were taken are shaded.

Localities :

- | | | |
|--------------------|--|-------------------|
| 1. Urchfont Hanger | 10. Wantage 1 | 18. Aston Rowant |
| 2. Broomsgrove | 11. Wantage 2 | 19. Bagley Wood |
| 3. Cobham Frith | 12. East Ilsley | 20. Hinksey Hedge |
| 4. Putall Gate | 13. Streatley South Wood | 21. Wytham Lane |
| 5. Rough Down | 14. Sowberry Court | 22. Wytham Woods |
| 6. Rockley 1 | 15. The Crown, Huntercombe | 23. Wytham Woods |
| 7. Rockley 4 | 16. Christmas Common (Wood and Downside) | 24. Canal Bank |
| 8. Hackpen | 17. Shirburn Lodge | 25. Parks Hedge |
| 9. Burdrop Wood | | |

In each locality, all the shells found in several small areas within the locality were collected, whether alive or dead, whole or broken, except that no shells less than half the adult size were taken (in fact, very few that were not adult) and that fragments were taken only when the complete band-formula could be determined from them, and it was obvious that each piece was derived from a different shell.

(ii) Recording

To give as much information on each shell as was practicable, von Martens' system (1832) of band-formulae was adopted with slight modifications, since more detailed systems were found to require disproportionate labour in recording. The bands are numbered 1 to 5, the uppermost being 1. Thus a five-banded shell is represented by 12345, a shell with the middle band only as 00300, and one with

no bands as 00000. Fusions are shown by bracketing the fused bands. As fusion may begin at almost any time in the growth of the shell, an arbitrary distinction must be made to avoid undue complexities. All bands fused at and after a line drawn across the body-whorl from the umbilicus at right angles to the lower lip of the mouth were considered as fused. This convention is illustrated in fig. 2. In a few specimens (all of them with brown shells) the bands could not be distinguished from the general shell-colour; these were classed as "banding indeterminable." Weakly pigmented bands which are interrupted in several places were represented by colons, and were considered as bands for the purpose of this paper. Bands present only as traces close to the lip were recorded as traces but disregarded for the classification employed here.



FIG. 2.—Convention used in classifying partial fusing. If fusion extended from the lip to the line shown or beyond, the bands were considered fused.

Ground colour was recorded as approximating to one or other of a series of shells chosen as colour standards and representing the commonest colours. The colour of the intact shell is either yellow or belongs to one of two series, both beginning with a fawn-brown, one leading to a deep sepia-brown, the other through orange-brown and dull pink to a dull red. These colours are the result of pigment in the calcareous layers of the shell showing through a thin, slightly brownish, yellow periostracum. Yellow shells have varying amounts of yellow pigment, medium brown and deep brown ones have a dull leaden violet. All the others have pink. We therefore distinguished three main colour groups, with yellow, violet, and pink-pigmented shells.

Some very pale fawn shells approach the yellow group, which otherwise is distinct and has not been subdivided. The pink series was broken up into three classes, fawns, pinks, and reds. Intermediates were placed in the class they most resemble. The browns vary from medium to dark, but subdivision has not been found necessary. Old shells that had lost the periostracum have been recorded separately.

It was noticed that as Taylor (1907-14) has pointed out, the ground colour of the shell is paler when there are several bands present than when there are few.

TABLE
Collections Classified

Locality	12345	(12)345	1(23)45	123(45)	(123)45	1(2345)	(12345)	(12)3(45)	1(23)(45)	(123)(45)	(12)(345)	02345	023(45)
Downland Beech—													
Hackpen
Rockley 1
Rockley 4
Crown Huntercombe	2
C. C. Wood	5	2	1
Aston Rowant
Shirburn Lodge
Urchfont Hanger
Total	7	2	1
Oakwood—													
Broomsgrove	6	6
Cobham Frith	10	...	1	3	1	...	12	1
Putall Gate	68	1	69	64	1	1
Total	84	...	1	4	1	...	87	65	1	1
Mixed Deciduous Wood—													
Wantage 1	4	1	4
Streatley S. Wood	20	...	2	2
Wytham	108	6	5	8	15	...	1	1	18	3
Bagley	13	1	...	2	1	1	1	...
Burdrop Wood	37	...	1	3	9	3
Wantage 2	15	2	...	1	2	9	...	1
Total	197	9	8	14	1	...	3	31	...	2	1	28	6
Hedgerows—													
Wytham Lane	13	1	1
Canal Bank	105	4	5	14	1	1	16	16	3	18
Parks Hedge	57	6	1	2	12
Hinksey Hedge	14	5	4	2	...
Total	189	10	6	21	1	1	17	33	3	18	...	2	...
Downside, Long Coarse Grass—													
Pentridge	283	5	4	4	7	6	4	...
C. C. Downside	54	1	...	13	9	1	11	5
Total	337	6	4	17	7	15	1	15	5
Downside, Short Turf—													
Rough Down	8
Other Stations—													
E. Ilsley	9
Sowberry Court	7	1	1	8	2	4	1	1
Totals	830	26	20	64	3	1	124	150	5	21	2	46	12

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y banding

02(345)	0(2345)	0(23)(45)	10345	12045	12340	10045	02340	00345	003(45)	00(345)	00045	000(45)	00340	00300	00000	Indeter- minate	Total
...	65	94	...	159
...	41	115	...	156
...	2	3	...	5
...	6	3	...	11
...	1	10	7	...	26
...	11	...	11
...	1	6	...	7
...	2	4	...	6
...	1	127	243	...	381
...	49	36	...	97
...	2	7	117	54	...	199
...	185	211	...	609
...	2	7	351	301	...	905
...	18	...	27
...	5	44	...	73
...	5	1	1	...	3	16	5	...	5	2	4	31	38	2	278
...	1	5	10	...	35
...	1	...	1	1	5	9	44	...	114
...	22	...	52
...	1	...	7	1	1	...	4	21	5	...	5	2	4	50	176	2	579
1	2	1	1	4	...	24
...	7	2	...	1	53	33	...	279
...	2	1	...	81
...	1	6	9	...	41
1	2	9	2	...	1	62	47	...	425
...	9	4	102	4	2	434
...	1	...	6	1	...	17	2	1	...	17	19	...	158
...	1	...	15	1	...	21	2	1	...	119	23	2	592
2	...	1	2	2	2	1	45	101	...	164
...	1	1	5	23	4	43
...	45	...	70
3	2	1	26	1	1	1	4	62	11	2	6	3	6	759	959	8	3159

(The colour divisions used above appear to correspond to the varieties described or illustrated by Taylor as follows :—

Yellows are all var. *libellula* Risso.

Fawns are var. *petiveria* Moquin-Tandon.

Pinks are var. *rubella* Picard in the strict sense.

Reds are var. *rubra* Baudon.

Browns include var. *castanea* Picard and var. *olivacea* Risso except that var. *petiveria* Moquin-Tandon is reduced by Taylor to a subspecies of var. *castanea* Picard in the wider sense. As its shell pigment is pink, not violet, it should be retained as a separate variety.

RESULTS

The results of our collecting are shown in tables 1 and 2. In these, the localities have been classified according to their broad ecological features. We have collected in six main types of habitat, downland beechwoods, oakwoods, mixed deciduous woods, hedgerows, downsides with long coarse herbage, and downsides with very short turf. Two localities not referable to any of these are listed separately.

The downland beechwoods are all pure beech. The woods at Aston Rowant, Shirburn Lodge and Christmas Common are dense, with a thick permanent carpet of tough red-brown beech leaves. Christmas Common and Aston Rowant have a small quantity of brambles (*Rubus* sp.). Undergrowth in dense beechwoods is very slight. The woods at Hackpen and Rockley 1 are more open, with much thin sparse grass, and an incomplete leaf-carpet with exposures of dark brown soil and small stones of chalk and flint. Rockley 1 is notable for the large quantity of fallen beech cupules (which are very dark brown). Hackpen and Rockley are in exposed situations, and wind is responsible for the incompleteness of the leaf-carpet. Urchfont Hanger has large drifts of leaves, alternating with bare areas. The collection from The Crown, Huntercombe, was taken from the edge of a beechwood, on a steep, dry, rather bare roadside bank overshadowed by the trees.

It will be seen from the tables that the average proportion of unbanded and one-banded shells is far higher in all the beechwoods investigated than in any other type of locality. The average proportion of yellow shells is much less than in downland grass or hedgerows, but higher than in oakwoods or in the two unclassified localities. It is rather similar to that for mixed deciduous woods, but it is almost entirely due to the collections from Hackpen and Rockley 1, which were rather open with some grass.

The oakwoods visited differ in density. Broomsgrove is a very dense oakwood with etiolated hazel shrubs and nothing but dead, brown, leaves on the ground. Cobham Frith was like Broomsgrove

TABLE 2
Collection classified by colour

Locality	Fresh shells					Old shells			Total
	Yellow	Fawn	Pink	Red	Brown	Colour unknown	Pink	Yellow	
Downland Beech—									
Hackpen	39	51	49	15	2	3	159
Rockley 1	42	14	25	9	66	156
Rockley 4	1	4	5
Crown Huntercombe.	...	3	3	3	2	...	11
C.C. Wood	8	15	3	26
Aston Rowant	4	4	3	11
Shirburn Lodge	2	3	1	1	...	7
Urchfont Hanger . .	1	...	3	2	6
Total	82	74	87	34	72	11	18	3	381
Oakwood—									
Broomsgrove	7	5	27	...	47	...	8	3	97
Cobham Frith	25	24	118	12	6	...	13	1	199
Putall Gate	22	293	174	33	59	...	28	...	609
Total	54	322	319	45	112	...	49	4	905
Mixed Deciduous Wood									
Wantage 1	8	15	3	1	27
Streatley S. Wood . .	6	15	33	4	8	...	5	2	73
Wytham	69	84	37	3	28	16	41	...	278
Bagley	6	8	15	2	4	35
Burdrop Wood	37	15	22	1	24	3	5	7	114
Wantage 2	14	1	29	...	8	52
Total	140	138	136	10	75	19	51	10	579
Hedgerows—									
Wytham Lane	16	3	1	...	1	1	2	...	24
Canal Bank	114	101	53	...	11	279
Parks Hedge	14	46	16	2	3	...	81
Hinksey Hedge	18	7	6	7	3	...	41
Total	162	157	76	...	12	10	8	...	425
Downside, Long Coarse Grass—									
Pentridge	277	1	127	...	26	...	3	...	434
C. C. Downside . . .	66	45	43	1	...	1	2	...	158
Total	343	46	170	1	26	1	5	...	592
Downside, Short Turf— Rough Down	74	8	17	...	65	164
Other Localities—									
E. Ilsley	6	1	35	1	43
Sowberry Court . . .	7	31	32	70
Totals	868	777	805	90	429	42	131	17	3159

but a large part was felled about four years ago, with a consequent invasion of rosebay willow-herb (*Epilobium angustifolium* L.) and some brambles. The collection was taken from this part. The willow-herb forms dense thickets of straight and very leafy stems about five feet high in summer. Putall Gate is rather more open than Broomsgrove and has some undergrowth of brambles and St John's Wort (*Hypericum* sp.).

The proportion of unbanded and one-banded shells in these woods is the third highest, only less than in beechwoods and Rough Down. The general colour is pinkish-brown with a very much higher proportion of fawns than in the beechwoods. The proportion of yellows is the lowest of any habitat investigated.

The woods classed as mixed deciduous are a heterogeneous group. Wantage 1 and Streatley South Wood have a high proportion of beech, and the collections from them approach those from beechwoods in their character. Wytham and Bagley may be regarded as typical of these localities. Both are composed of a mixture of oak, ash, sycamore and other deciduous trees, with a certain amount of shrubs and with a plentiful undergrowth of brambles, bracken, grasses and woodland herbs. Bagley is the denser but neither is as dense as any of the oakwoods or beechwoods. Conifer plantations in Bagley were not visited. Burdrop Wood has a high proportion of ash and lies on an extremely steep Lower Chalk-escarpment. Here, the collection was taken from an area containing much hazel and sloe with an undergrowth of brambles and nettles. Wantage 2 was a small open copse of elms on bare stony ground with young elm scrub and a little grass.

The proportion of unbanded and one-banded shells is much lower in mixed deciduous woods than in any other locality so far considered, but it is higher than in hedgerows and downland with coarse grass. The proportion of yellows is also high although less than in hedgerows and downsides. Yellows, fawns and pinks are approximately equally common.

The hedgerows are all principally of hawthorn with few and widely-spaced trees. All are bordered by rank green herbage, except the Parks Hedge which had been neglected and had a thick outgrowth of brambles, beneath which there was little green vegetation.

The average proportion of yellows in the hedgerows is higher than for any but downside localities (and it may be noted that the lowest proportion in any Hedge was found in the Parks Hedge collection). The proportion of unbanded and one-banded shells is the lowest except for downside with coarse grass, the difference between the two being very small.

The downside habitats all consist of herbage, sometimes with scattered bushes (usually hawthorn), on very thin soil above pure chalk, and all are on steep slopes. Christmas Common downside has scattered hawthorn bushes, and long coarse grass with a strong

mixture of rough herbs. The ground is broken in places, chiefly by the action of rabbits. The collection from the Pentridge (near Cranbourne, Dorset) was obtained through Dr D. A. Darcy, and the site has not been visited by us. From Dr Darcy's description it resembles Christmas Common downside strongly. It is a considerable distance from all the other stations, and may possibly be subject to slightly but significantly different climatic conditions. The proportion of unbanded and one-banded shells in these localities is the lowest observed, the proportion of yellows the highest.

Rough Down agrees with the other downsides in its general features, but there are no bushes near the collecting-area. The vegetation is extremely short cattle- and rabbit-grazed turf, and has been so for at least forty years. The ground is broken in many places through the action of moles, cattle, and rabbits on the very steep downside, and there are a number of chalk and flint stones, the former white, the latter dark brown or grey. The percentage of unbanded and one-banded shells is second only to that from beechwoods; the percentage of yellow second to that from downside with coarse grass.

The remaining two localities differ from those described above. The collection from East Ilsley was taken from among thick, long, dull-green, very uniform grass on a bank at the side of a downland track. The bases of the grass clumps were thickly clothed with dead leaves and stems so that the colour of the vegetation at the soil surface was uniformly brown. The shells were found in this layer, several showing evidence of predation by rats. The collection contained a high proportion of unbanded shells and a lower proportion of yellows. Nearly all the shells were brown. The collection from Sowberry Court was from a very neglected downland hedge that had widened and become almost a copse. There was very little undergrowth, the soil being covered with beech leaves and mast, larch cones and needles, and dead hawthorn leaves, all forming a dark brown carpet. There were many rabbit burrows. This collection had a very high proportion of brown shells and very few yellows. The proportion of unbanded shells was high; there were no one-banded shells.

DISCUSSION

It is obvious from tables 1 and 2 that there is a close relationship between the ratios of the colour and banding-patterns in any colony and the sort of background on which it lives. If one chooses the five localities with the most green vegetation at ground level, and the five with the most brown or red-brown carpet, the lowest percentage of yellow shells in any of the green habitats is 41 per cent. (114 in 279), the highest in the browns is only 17 per cent. (1 in 6), as shown in table 3. Intermediate habitats tend to intermediate values. To compare banding and discontinuity of background one must select

the five most uniform backgrounds, and the five showing greatest discontinuity. The results are shown in table 4. The lowest percentage of unbanded shells on a uniform background is 59 per cent. (94 in 159), the highest in variegated backgrounds is 22 per cent. (9 in 41). A general tendency to loss of bands is shown when one considers not only unbanded shells, but one-banded (00300) and those without

TABLE 3

Relation between greenness of background and percentage of yellow shells

Locality	Per cent. yellow shells	No. of shells in collection
<i>(a) Greenest</i>		
Wytham Lane	76	24
Pentridge	64	434
Rough Down	45	164
Christmas Common downside	43	158
Canal Bank	41	279
<i>(b) Least Green</i>		
Urchfont Hanger	17	6
Broomsgrove	8	97
Putall Gate	4	609
Aston Rowant	0	11
Shirburn Lodge	0	7

TABLE 4

Relation between uniformity of background and percentage of unbanded shells (00000)

Locality	Per cent. unbanded shells	No. of shells in collection
<i>(a) Most uniform</i>		
Aston Rowant	100·0	11
Rockley 1	74·0	156
East Ilsley	62·5	43
Rough Down	61·5	164
Hackpen	59·0	159
<i>(b) Least uniform</i>		
Hinksey Hedge	22·0	41
Wytham Lane	17·0	24
Christmas Common downside	12·0	158
Canal Bank	12·0	279
Parks Hedge	1·2	81

bands 1 and 2 as well. Bands 4 and 5 are not normally visible to any great extent and can vary without affecting the appearance of the living snail. Shells with such formulæ as 12300 can be classed with 12345 as effectively five-banded. The results of considering effective banding are shown in table 5. The lowest percentage of

effectively unbanded shells on uniform backgrounds is 79 per cent. (34 in 43) and the highest against a broken background is 39 per cent. (16 in 41).

TABLE 5

Relation between uniformity of background and percentage of effectively unbanded shells

Locality	Effectively 12345	Effectively 00000	Per cent. 00000
(a) <i>Most uniform</i>			
Aston Rowant . . .	0	11	100
Rockley 1 . . .	0	156	100
East Ilsley . . .	9	34	79
Rough Down . . .	11	153	93
Hackpen . . .	0	159	100
(b) <i>Least uniform</i>			
Hinksey Hedge . . .	25	16	39
Wytham Lane . . .	18	6	25
Christmas Common downside	102	56	35
Canal Bank . . .	192	97	34
Parks Hedge . . .	78	3	4

In fig. 3 is shown the relation between the percentage of effectively unbanded shells and the percentage of yellow shells for each locality. The connection between density of trees, high percentage of effectively unbanded shells, and low percentage of yellow shells, which corresponds to the relation between density of trees, uniformity of ground-litter and lack of green vegetation at ground level, is obvious. As the woods become more dense, their resemblances to each other in these respects increase, and the variation within the colonies of *Cepæa nemoralis* inhabiting them decreases correspondingly. Hedgerows appear as very reduced and very variable woods, those with most bramble being most like the rest of the woodland series, with respect to colour. Excepting that from East Ilsley, colonies from downside with long grass resemble those from the greener hedges. Rough Down is unlike all the others in that it is grazed. Consequently its vegetation is green but very short, and uniform. The colony on Rough Down is very similar in lack of banding to the beechwood and dense oakwood colonies.

It is our experience in collecting that heavily banded shells are more conspicuous than unbanded ones in uniform localities, whereas unbanded ones tend to be conspicuous in hedgerows and similar places. Also, if all the shells from a given locality are considered, it is seen that the general ground colour corresponds closely with the general colour of the background (except that hedgerow collections tend to be of yellows and pinks). For example, the proportion of fawns to pinks is much greater in unfelled oakwoods than in any beechwood. This close relationship is in fact much greater than is

shown by our simple classification into yellows, fawns, pinks, and so on, but is difficult to estimate colorimetrically.

The results obtained could be affected by two principal factors. First, we are, no doubt, not perfect collectors and the collections might have an undue proportion of shells appearing conspicuous to us. Secondly, in many localities quantities of shells collected originally by predators (thrushes, rats, grey squirrels, small field rodents, and rabbits) have been included in our collections. But

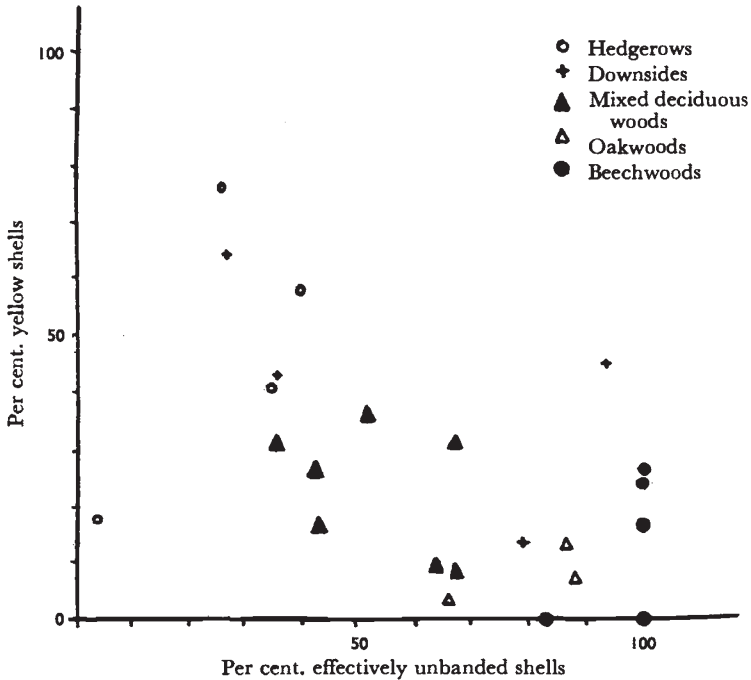


FIG. 3.—Relation between percentage of yellow shells and percentage of effectively unbanded shells in each locality. Note that localities classified together because of their ecological similarity (*e.g.* downland beechwoods or hedgerows) tend to group together. Sowberry Court has been included in the mixed deciduous woods, and East Ilsley in the downsides.

both these effects should, if operative, tend to obscure the correspondence which we have shown, and cannot increase it.

An explanation of the correspondence between background and colour-pattern of shell must be found. It has been stated (see, *e.g.* Taylor, 1907-14, p. 288) that shell coloration depends on the food-plants. But it has been observed by Lang (1904, 1912), Fisher and Diver (1934) and ourselves that colour is genetically controlled, and, further, that animals with shells of the most diverse colours, when all fed on the same food, *e.g.* lettuce, continue to add segments of the original colour to the growing shell. One does not find in nature shells showing numerous cross-bands of different colours. It is even

more difficult to explain the differences in banding on the grounds of difference in diet, and again, Lang (1904) and others have observed genetical control of the banding-patterns.

It has been suggested by Diver (1940) that differences between the colonies might well be due to genetical drift, along the lines indicated by Sewall Wright (*e.g.* 1940). But it is exceedingly improbable that if the colonies visited by us were all showing random divergence, all the beechwood colonies, for example, should have reached by chance such a remarkable similarity in stations often so many miles apart, especially while differing from those in other types of locality, which also show great similarities within the same locality-class.

The only other explanation which will account for this correspondence is natural selection acting upon genetic variation. *Cepæa nemoralis* is eminently polymorphic, so that one would expect a balance of different genetic forms in each population, maintained by the physiological advantage of certain gene-combinations but with the actual ratios of genotypes altered in different directions in different situations by the action of natural selection. Consequently the details of the results obtained in this survey cannot be assumed, without further investigation, to apply to colonies in widely distant parts of Britain, since differences in climate may well result in different physiological advantages of particular gene-combinations and so set up a different initial balance. (For example, unbanded pink shells might perhaps be more abundant in Cornwall because of a different physiological balance in that climate, but one would expect to find the relative proportions in different types of localities to be much as in the district investigated by us.) To determine the balance, the different localities chosen must be within a reasonably restricted area, otherwise an unknown part of the differences observed will be caused by changes in physiological advantage associated with difference in climate.

Although much work has been done on the genetics of *Cepæa nemoralis*, little of it appears to have been published. Haldane (1932) states that variations in the patterns are due either to multiple allelomorphism or to very closely linked sets of genes, but gives no evidence. From the work of Lang (1904, 8, 11, 12) and Fisher and Diver (1934) it appears that yellow is recessive to other colours, and the possession of bands is recessive to the lack of them. The results of Stelfox (1918) are open to the objection that he started with adults that may well have been previously fertilised. His F_2 generations point to linkage between colour and banding, but unfortunately the numbers given are too small to be significant. Fisher and Diver (1934) have shown linkage between colour and banding, apparently of varying degrees of closeness. From our study of the shells it appears that the 00300 condition is distinct from other bandings, and without intermediates, so that it is probably controlled by a

simple Mendelian mechanism. Intermediates can be found between most if not all of the other bandings. Breeding experiments are being undertaken to investigate these points.

In the course of our collecting, plentiful evidence has been obtained of predation by thrushes, grey squirrels, rats, small field rodents, and rabbits. No complete investigation has so far been made into the different intensities and kinds of selection by these animals. Experiments are in progress, but it should be pointed out that if selection is of the order of 1 per cent., which is considered large by Fisher (1930*b*), it may be almost impossible to demonstrate by normal sampling methods, but of course it may fluctuate considerably, and in consequence be easily detectable over short periods. It is also necessary to know the area from which the predators are collecting and the exact composition of the snail population within it, for which reason, as Robson and Richards (1936) have pointed out, the work of Trueman (1916) and Haviland and Pitt (1919) is inconclusive. The population can be estimated numerically by recapturing marked animals. We have already found a suitable marking technique for this purpose. The results obtained with it will also provide the necessary information on the distance which the predators carry the snails. Cott (1940) has shown that it is unnecessary to demonstrate that these predators have colour vision since tone is as important as colour.

Diver (1929) has shown from examination of fossil specimens that this species has been polymorphic at least since the Neolithic period. He concludes that the frequencies of different types of banding have remained approximately constant since then, but since the habitats occupied by his fossil specimens are unknown, this conclusion can be accepted only with the greatest reserve. It does not follow that other populations coeval with those of the Neolithic collection, for example, would also show the same banding-frequencies unless these were from the same sort of habitat.

Polymorphism in this species is therefore normal and stable. In every colony investigated by us (except one from which a sample of only 11 shells was obtained) at least two, and more usually five or more different phenotypes were observed, so that the various colonies are distinguished by ratios of phenotypes, not by the complete fixation of a single phenotype in each colony.

There are four principal types of polymorphism that could concern us here. Either an advantageous gene is spreading through a population (Ford, 1940, pp. 493-4), or there is balanced polymorphism with the heterozygote at an advantage (Fisher, 1930*b*), or particular gene-combinations are stabilised by linkage so that the recombination classes are infrequent (Haldane, 1930; Fisher, 1930*a*; Ford, 1940), or one may have numerous populations showing random fluctuations as Sewall Wright suggests (*e.g.* 1940) and moving towards fixation of particular genes. The first and last possibilities are extremely

unlikely because the polymorphism appears stable, and the probability on either hypothesis of obtaining such a relationship as we have shown above is remote. Both the second and third agree with our results. Linkage has been shown by Fisher and Diver (1934) and by Stelfox as quoted by them.

In table 6 is shown the distribution of banding with respect to colour for most of our collections. The distribution of the different forms of banding is often not the same within the different colour

TABLE 6

(Only fresh shells were reckoned in compiling this table)

Locality	Yellow					Pink					Brown				
	00000	00300	12345	Others	TOTAL	00000	00300	12345	Others	TOTAL	00000	00300	12345	Others	TOTAL
Downland Beech—															
Hackpen . . .	15	24	39	76	39	115	1	1	2
Rockley 1 . . .	17	25	42	41	7	48	57	9	61
Oakwood—															
Broomsgrove . . .	1	4	1	1	7	5	22	4	1	32	30	15	1	1	47
Cobham Frith	24	1	...	25	51	80	7	16	154	...	4	1	1	6
Putall Gate . . .	9	6	4	3	22	135	165	62	138	500	59	59
Mixed Deciduous Wood—															
Streatley S. Wood . . .	2	1	3	...	6	33	4	11	4	52	8	8
Wytham . . .	1	7	33	28	69	15	15	54	40	124	24	6	30
Bagley	4	2	6	6	5	9	5	25	4	4
Burdrop Wood . . .	1	4	18	14	37	17	3	8	10	38	23	1	24
Wantage 2 . . .	7	...	3	4	14	7	...	12	11	30	8	8
Hedgerows—															
Wytham Lane . . .	2	1	10	3	16	2	2	4	1	1
Canal Bank . . .	17	25	46	26	114	7	27	59	61	154	9	1	...	1	11
Hinksey Hedge . . .	5	2	5	6	18	4	1	5	3	13
Parks Hedge . . .	1	1	10	2	14	...	1	42	19	62
Downside, Long Coarse Grass—															
Pentridge	66	185	23	274	...	32	82	11	125	8	2	12	6	28
C. C. Downside	11	21	34	66	19	6	33	31	89
Downside Short Turf—															
Rough Down . . .	47	21	...	6	74	5	13	...	7	25	49	11	...	5	65
Other Stations—															
E. Ilsley	6	...	6	...	1	1	27	4	2	2	35
Sowberry Court . . .	1	...	2	4	7	12	...	5	14	31	32	32

classes. They are materially different in Rockley 1, Burdrop Wood, and Christmas Common downside, for example. (Banding in brown shells is usually extremely weak and difficult to determine except in some shells with formula 00300. It appears that there is interference by the colour factors in the expression of the banding-factors, so that brown shells must be disregarded for this purpose.)

Consider two pairs of alleles neither autosomally linked nor sex-linked. If one pair is in the ratio $p : q$, then in the absence of selection, in a very large population the ratio of genotypes in the next generation will be

$$p^2 (AA) : 2pq (Aa) : q^2 (aa).$$

The situation is the same for the other pair. Let the ratio be

$$p_1^2 (BB) : 2p_1q_1 (Bb) : q_1^2 (bb).$$

If the progeny are classified by their constitution with respect to A and a, then as there is no linkage, the members of each class (AA or Aa or aa) should be in the ratio

$$p_1^2 (BB) : 2p_1q_1 (Bb) : q_1^2 (bb).$$

Now if selection of any sort is acting, let the selective advantages of AA, Aa and aa be respectively $x : y : z$, and for BB, etc. $x_1 : y_1 : z_1$. Now the ratios of genotypes in the next generation will be given by the expression

$$(xp^2 (AA) + y2pq (Aa) + zq^2 (aa)) (x_1p_1^2 (BB) + y_12p_1q_1 (Bb) + z_1q_1^2 (bb))$$

If these are now classed as phenotypes we have :

A and B	A and b	a and B	a and b
$xp^2x_1p_1^2 (AABB)$	$xp^2z_1q_1^2 (AAbb)$	$zq^2x_1p_1^2 (aaBB)$	$zq^2z_1q_1^2 (aabb)$
$2xp^2x_1p_1q_1 (AABb)$	$2ypqz_1q_1^2 (Aabb)$	$2zq^2y_1p_1q_1 (aaBb)$...
$2ypq x_1p_1^2 (AaBB)$
$4ypqy_1p_1q_1 (AaBb)$

Whence it is easily seen that the ratio of B to b in class A is still the same as in class a. Consequently selection acting directly upon independent gene pairs cannot disturb this ratio. However, if there is interaction between the gene pairs (so that the selective advantage of any genotype is not simply derived from those of its genes) this situation will not hold. Physiological selection on genes only, not on genotypes, seems unlikely in these snails since the discrepancy between the ratios is in different directions in different colonies and is too large. Selection (by predation) of different phenotypes seems more likely. If so, since there will be continual recombination in each generation, all discrepancies must be produced by selection within the lifetime of each generation. In this case, selection must be fairly heavy, and easily detectable. But linkage may well be present. If so, and it is not very close, then the observed discrepancy will not be found without selection, since the less common classes will be increased by crossing over (from the commoner classes) more rapidly than they are decreased by it. If linkage is very close, the discrepancy might be expected, but our results do not suggest such a state of affairs.

With linkage and selection the discrepancy can be expected and will accumulate slowly until balanced by recombination. In this case, the amount of selection in each generation may be very small and difficult to detect. Our present collections are not large enough to allow any determination of the relative importance of physiological selection and selection by predators, but do show the importance of selection in general. Further evidence is being obtained from experiments involving breeding, and sampling natural and artificial populations.

Diver (1939, 1940) has shown that *Cepæa nemoralis* and *C. hortensis* are found in small breeding-communities, each containing considerably less than 100 individuals, within a colony. Particular patterns may be found only within one such community, or in a few close together. This non-random distribution he ascribes to genetical drift. Our observations in the field are in agreement with this explanation, but with the important proviso that the general facies of each colony is determined by selection, in part at least through the action of predators and in correlation with the background. Consequently, the degree to which any single breeding community can drift is limited. Within the range of our observations, drift cannot act against natural selection.

Cepæa nemoralis has been quoted by Haldane (1932), Robson and Richards (1936), Dobzhansky (1941), Huxley (1942), and Mayr (1942) on the evidence of Diver as giving an example of random distribution of varieties, the patterns of which have no selective value.

It is regrettable that most of the evidence from which widely quoted conclusions on this species were originally drawn remains unpublished and therefore inaccessible to zoologists in general.

Crampton's papers (1916, 1925, 1932) on the genus *Partula* are often quoted as giving evidence of random variation resulting from genetic drift. A close examination of them does not support this view. His very full data give good indications of clines in at least two species. Several species have extended their range; this points to considerable migration. In one species, evidence is given that the proportions of certain varieties fluctuated markedly between the years 1906 and 1909. These fluctuations seem much too large to be caused by drift. Crampton's data are usually for whole valleys, sometimes for a third of a valley; they are taken not from small isolated communities within a population, but from the population as a whole, which in many cases must be large. All these considerations tend to reduce the value of his data for suggesting the action of drift; in fact, much of the evidence he produces suggests that natural selection is operating.

Welch's work (1938) on *Achatinella mustelina* Mighels is also widely quoted as a parallel. Welch gives no indication of the nature of the backgrounds on which this arboreal snail is found, nor of its predators. Looking through his illustrations, one gets the impression that this

species is remarkably variable, much as is *Cepaea*. His paper does not give the necessary data for conclusions on drift.

It seems that in view of the results presented above, all such cases of polymorphic species showing apparently random variation should be reinvestigated. No useful conclusions on this matter can be drawn merely from a knowledge of the distribution of varieties without a study of their habitats.

Diver (1940) has claimed that variations in shell colour and banding in the snail *Cepaea nemoralis* (L.) have no selective value, and occur at random in different colonies. He ascribes the differences between colonies to genetical drift.

These contentions cannot be sustained. There is a definite relationship between the proportions of different varieties in any colony, and the background on which they live. The more uniform the background (*e.g.* a continuous leaf-carpet, or an expanse of very closely grazed turf) the higher is the number of unbanded shells. Pink, fawn, red and brown shells vary in numbers and exact shade according to the general colour of the background. The proportion of yellow shells increases as the amount of green vegetation at ground level increases.

Thus there is good evidence that the general appearance of any colony is determined by natural selection. Predation is by thrushes, rats, squirrels, small field rodents, and rabbits. The close correspondence between the general appearance of each colony and its background suggests that predators hunting by sight are the agents of selection.

Polymorphism in this species is normal and stable, and is probably maintained by the physiological advantage of certain gene-combinations. The proportion of different forms of banding within the various colour classes are not always the same in any one colony. Consequently there must be either very close linkage between colour and banding, or linkage in some degree combined with selection for particular genes, or differential elimination of phenotypes, the last being probably the most important. Each colony is maintained in a state of stable polymorphism, but the proportions of the varieties are determined by natural selection. Whatever genetical drift may occur cannot act against natural selection, and is severely limited by it.

Cepaea nemoralis has been widely quoted as an example of a polymorphic species showing random distribution of non-adaptive genes. The work of Crampton on the genus *Partula* and of Welch on a species of *Achatinella* has also been quoted as giving evidence of genetical drift. The papers of these authors, however, provide no evidence for drift and in one instance give some evidence for selection. In view of this, all situations supposedly caused by drift should be reinvestigated.

SUMMARY

1. Collections of the land snail *Cepæa nemoralis* were taken from various localities in southern England.
2. The ground colour and band-formula of each shell was recorded.
3. Localities were classified into six main types according to their broad ecological features and the percentages of the different colour- and banding-varieties, found at localities in different ecological situations, were compared.
4. It was shown that there was a close relationship between the ratios of the colour and banding-patterns in any colony and the sort of background on which it lived.
5. Colonies of *C. nemoralis* living in the same type of ecological habitat tend to resemble one another, but those from different types of habitat tend to differ.
6. Selection, through the agency of predators hunting by sight, acting upon a stable polymorphic situation was shown to be the most important factor determining the general appearance of different populations.
7. Colour and banding patterns are genetically controlled and the species is stably polymorphic.
8. Linkage between colour and banding has been shown, but the difference in the distribution of banding-patterns in each colour class is probably the result of differential elimination of phenotypes.
9. It was suggested that all polymorphic situations, supposedly caused by drift, should be reinvestigated.

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