NATURAL SELECTION IN CEPAEA

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THE remarkable variation in colour and ornamentation of the shell which is shown by certain gastropods has attracted the attention of collectors for many years. Recently, several studies of this variation have appeared, which unfortunately lead to very diverse conclusions on its mechanism of maintetenance and its significance in evolution. One of the commonest and most strikingly variable snails of Europe is *Cepaea nemoralis,* which has been studied in considerable detail by several workers, mainly in Europe but also in the U.S.A. where it has been successfully introduced. DIVER (1940) has concluded that its range of variation is wholly random, BOETTGER (1931) that on the contrary it is determined by natural selection, while LAMOTTE (1951) believes that for banding, at least, it is maintained in each colony primarily by mutation, and SCHILDER (1950) by gene flow.

Our own investigations (CAIN and SHEPPARD 1950, 1952; SHEPPARD 1951, 1952) lead us to the conclusion that variation is maintained by balanced polymorphism (FISHER 1930a; FORD 1940), but the proportions of different varieties in each colony are strongly affected by selective visual predation. In this paper the principal studies on *Cepaea nemoralis* are examined, and further evidence for the importance of natural selection is presented.

SYSTEMATICS

The genus Cepaea Held 1837, proposed and still often ranked as a subgenus of Helix L., contains four very closely allied species, reviewed by PERROT and PERROT (1938). *C. vindobonensis* is confined to southeastern Europe and the Caucasus, *C. sylvatica* to the western Alps. *C. hortensis* ranges through north, central and western Europe from Finland to the Pyrenees, and the British archipelago, and as far as Iceland and northeastern North America. *C. nemoralis* is confined to central and western Europe from northern Italy (LAMOTTE 1951, p. 45) and Czechoslovakia to the Pyrenees, Ireland, south Scotland and southern Scandinavia. It has been introduced into Canada, the United States, and New Zealand. All these species overlap geographically except the closely allied *C. sylvatica* and *vindobonensis,* but *sylvatica* is a high mountain form, probably isolated by altitude from all the others, according to the data given by LAMOTTE (1951). *C. sylvatica* and *vindobonensis* both have a haploid chromosome number n = 25, *C. hortensis* and *nemoralis* have n = 22 (PERROT and PERROT 1938). Hybridization between *C. nemoralis* and *hortensis* has been

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well reviewed by LAMOTTE (1951). It is extremely rare in the wild. Hybrids have been produced with some difficulty in the laboratory (LANG 1904, 1912; KLEINER 1912). DIVER (1940) observed courtship between individuals of *hortensis* and *nemoralis* and concluded that specific differences in courtship behaviour probably formed an efficient barrier to fertilization.

POLYMORPHISM

Although all the species of Cepaea are variable in shell characters, *C. nemoralis* is particularly so. The lip is normally black or dark brown, rarely pink or white. The rest of the shell may be yellow, brown or any shade from very pale fawn through pink and orange to red. Up to five black or dark brown (seldom transparent) longitudinal bands may be present, very rarely more. All possible combinations of presence or absence and of fusion of adjacent bands have been recorded (TAYLOR 1914), but their frequencies vary considerably; particularly common are five-banded, and unbanded shells and those with only the middle band. For recording, the bands are numbered 1 to 5, the uppermost being 1. Fusions are indicated by bracketing the numbers representing the fused bands, absence by 0. This system is slightly simplified from that proposed by VON MARTENS (see LAMOTTE 1951). The bands may vary greatly in width, and also in their point of origin along the shell. A band may be absent or nearly absent either because it has been reduced in width to the vanishing point, or because its formation has been postponed until the animal has nearly or quite stopped growing. Fusions also may occur at any time after the appearance of the bands affected. In his monographic study of variation in *C. nemoralis,* LAMOTTE (1951) classifies the banding varieties by the presence or absence of bands, ignoring fusions. Apparently, a band is counted as present even if reduced to a mere trace near the lip. In our papers, these traces if appearing only for one-fourth inch or less and only close to the lip, are not recorded as present, since they are phenotypically almost insignificant. Fusions are recorded only if they occupy a large part of the largest whorl of the shell (CAIN and SHEPPARD 1950).

Although most of the various banding-varieties grade into each other because of variation in the development and fusion of bands, some appear clear-cut. The unbanded form 00000, and that with only the median band, 00300, are usually distinct from the five-banded ones (12345 with or without fusion), intermediates with more than the slightest traces being very rare. On the other hand, every intermediate due to reduction in width of bands between 12345, 02345, 10345, 00345 and 00045 may occur in the same colony. In some colonies, however, certain of these combinations may occur without intermediates. The intensity of pigmentation of the bands varies somewhat; rarely there occurs a very distinctive variety in which there is no dark pigmentation. Although the ground colour is present, these individuals are referred to in the literature as albinos. The bands are transparent and tinged with the ground colour of the shell, and the lip is white or pink.

There are three distinct colour classes. The calcareous layers of the shell are suffused with yellow, pink, or dull violet which in combination with the yellow proteinous periostracum produce respectively yellow, a range of colours from fawn to red, and dull brown. LAMOTTE (1951) appears not to have found examples of the last class.

In almost every colony, at least two colour and banding classes are represented, and frequently many more. The compositions of many French colonies are given by LAMOTTE (1951) and of some English ones by us (1950, 1952).

GENETICS

The earlier work on Cepaea has been admirably reviewed by LAMOTTE (1951) who has added considerably to the available information. It is certain that yellow ground colour is recessive to pink. The genetics of brown are not known. In our experience it is a clear-cut character almost certainly controlled by a single factor (see p. 96). The unbanded form 00000 is dominant to both 12345 and to 00300 which itself is dominant to 12345. It is highly probable, although not proved, that 00300 is not an allelomorph of 12345. LANG (1912) for *C. nemoralis* and BOETTGER (1950a) for *C. hortensis* have suggested dominance relations for 00345 and 00045, but do not give the necessary data. The character " pale or interrupted bands " as against the normal darkly pigmented and continuous ones has been studied by LANG (1908, 1912) and by LAMOTTE (1951) whose data support LANG's suggestion that it is controlled by a dominant gene, which is not an allele of colour or the various banding patterns. The character albino is recessive to normal pigmentation (of the lip and of bands when present). We can find no data to show whether it is an allele of " pale bands " or not: it is certainly not allelic with colour or banding patterns.

FISHER and DIVER (1934) have shown linkage between colour and banding with a crossover value of approximately 20%. STELFOX (unpublished data quoted by them) found the same linkage but with a crossover value significantly less than FISHER and DIVER's: in fact, in his experiment he observed no crossing over. Pink and yellow, and unbanded and some unspecified banding variety were investigated. FISHER and DIVER suggest that either the factors for pink were not the same in their and STELFOX's experiments, or that the closeness of linkage varies; presumably they and STELFOX used the same banding variety, otherwise this also could have differed. PROFESSOR J. B. S. HALDANE has suggested to us that the differences in crossover value may be associated with inversions. Unfortunately the chromosomes (figured by PERROT and PERROT 1938) are not good material for investigating this cytologically.

Linkage cannot normally be demonstrated from random samples of wild populations, but if it is very close, or there is selection for certain linked combinations, it can be observed. A striking deficiency of certain combinations without linkage could be brought about only by extremely heavy selection or by nonrandom mating. After extensive experiments, LAMOTTE (1951) has been unable to find any evidence of mating nonrandom with respect to colour and banding varieties of *C. nemoralis.* The data of SCHNETTER (1950) and SCHILDER (1926 and 1950) confirm this conclusion. DIVER (1932) has already

TABLE 1

Albinos

Locality		Yellow			Pink			Brown			Totals	Total
		00000	00300	Others	00000	00300	Others	00000	00300	Others		
Ballyness Bay	Normal	35	0	29	0	0	0	0	0	0	64	72
	Albino	0	0	8	0	0	0	0	0	0	8	
Thruxton	Normal	0	0	0	2	86	10	24	5	0	127	156
	Albino	0	0	0	0	29	0	0	0	0	29	
Pentridge I	Normal	0	63	196	1	34	93	6	2	18	413	428
	Albino	0	3	12	0	0	0	0	0	0	15	
Pentridge II	Normal	0	24	43	2	17	46	1	3	5	141	150
	Albino	0	3	6	0	0	0	0	0	0	9	

pointed out that linkage can be observed in wild populations of *C. nemoralis* and states (unfortunately without giving data) that all the shell characters investigated by him are linked. Our data tend to support this view, as will be seen from tables 1–6.

TABLE 2

Locality	Yellow			Pink			Brown			Total	Effectively unbanded except 00000 and 00300	00000 with traces in samples of more than 50
	00000	00300	Others	00000	00300	Others	00000	00300	Others			
Beechwoods												
Ashbury	0	0	3	5	1	5	17	0	0	31	0	....
Great Beech Wood	1	1	0	34	23	22	19	0	0	100	2	0
Beechgrove Farm Wood	0	0	5	31	0	16	7	0	0	59	0	1
Great Bear Wood	0	1	1	4	5	7	3	0	0	21	0	....
Pulpit Hill (top)	0	0	2	29	0	4	0	0	0	35	0	....
Rockley 1	1	5	0	4	1	0	8	1	1	21	0	....
Rockley 2	18	16	0	51	7	0	45	2	0	139	0	0
Rockley 6	9	4	0	8	19	0	43	0	0	83	0	0
Rockley 8	2	4	0	6	4	1	12	1	0	30	0	....
Rockley 9	1	3	0	2	6	1	9	3	0	25	1	....
Hackpen	15	24	0	78	39	0	1	1	0	158	0	18
Aston Rowant	0	0	0	23	0	7	0	0	0	30	1	....
Oakwoods												
Great Bedwyn Wood	1	2	0	3	13	0	2	0	0	21	0	....
Putall Gate	9	7	8	146	188	211	62	0	1	632	7	51
Boarstall Wood	0	0	0	54	28	51	0	0	0	133	0	6
Oakley Wood	0	2	4	8	41	72	0	0	0	127	3	7
Tackley Heath Wood	0	28	32	79	51	60	0	0	0	250	4	0
Stanton St. John Gt. Wood	0	0	0	5	7	10	0	0	0	22	0	....
Hell Coppice	0	2	0	10	27	16	3	0	0	58	0	1
Cobham Frith	0	25	1	54	88	25	0	4	2	199	0	24
Broomsgrove	1	4	5	5	30	5	30	15	2	97	0	12

It is not always possible to distinguish between a nonrandom distribution of characters due to linkage, and to multiple allelomorphs. Furthermore if the expression of an allele at locus A is dependent on the presence of a particular allele at locus B, and B is linked to a third locus, C, but not to A, nevertheless A may appear to be linked to C. This situation also cannot always be identified from such data. We will therefore refer to nonrandom distribution due to any of these situations as *associations* between the characters concerned.

TABLE 3

Locality	Yellow			Pink			Brown			Total	Effectively unbanded except 00000 and 00300	00000 with traces in samples of more than 50
	00000	00300	Others	00000	00300	Others	00000	00300	Others			
Mixed deciduous woods												
Filchamstead Wood	0	19	9	21	59	23	8	0	0	139	0	1
Pusey Common Wood	1	0	19	45	1	31	69	0	0	166	0	0
Little Wittenham Wood	3	0	9	69	12	67	63	0	0	223	3	13
Burdrop Wood	1	5	38	17	3	23	23	1	0	111	5	16
Wantage I	2	0	7	13	0	2	3	0	0	27	0	....
Wantage 2	7	0	7	7	0	23	8	0	0	52	0	3
My Lady's Seat, Wytham	39	14	117	91	31	217	105	0	0	614	143	2
Hen Wood	5	34	37	2	47	80	0	0	0	205	7	0
Wytham Hill Top	20	8	28	30	17	68	17	0	0	188	16	0
Spindle Trees, Wytham	11	15	28	31	51	120	34	0	0	290	45	5
Reserve Ride, Wytham	15	7	18	39	35	108	17	0	0	239	23	0
Lord's Common, Wytham	1	4	32	3	15	69	20	0	5	149	25	2
Streatley South Wood	2	4	11	84	11	33	17	0	0	162	0	24
Marley Wood, Wytham	4	74	329	210	146	662	83	0	0	1508	158	2
Common Piece Spruces, Wytham	9	19	42	94	87	197	14	0	0	462	40	2
Rockley Copse Cumnor	0	1	10	10	4	71	8	0	0	104	9	3
Marley Bog, Wytham	4	25	91	91	69	221	58	0	1	560	49	3
Bagley Wood	0	8	23	19	26	72	19	0	0	167	2	7
Blackwater Wood	0	1	3	7	5	18	1	0	0	35	0	....
Stanton Little Wood	0	4	3	3	2	12	0	0	0	24	0	....
Gt, Copse, Chislehampton	106	0	65	3	1	18	21	0	0	214	1	0

In table 1 are shown the only colonies we have found in which albinism is sufficiently frequent for association to be investigated. No unbanded albinos appear in it, but they have been found by us, and are reported by BOETTGER (1931) and LAMOTTE (1951). It is clear from the table that albinism is associated with colour and with the 00000 locus.

TABLE 4

Locality	Yellow			Pink			Brown					
	00000	00300	Others	00000	00300	Others	00000	00300	Others	Total	Effectively unbanded except 00000 and 00300	00000 with traces in samples of more than 50
Hedgerows												
Little Wittenham	11	1	43	6	0	54	17	0	1	133	2	0
University Farm	31	16	92	18	0	33	5	0	0	195	21	0
Bletchingdon Road	2	2	8	3	0	22	1	0	0	38	3	....
Shrivenham	0	1	93	1	0	16	9	0	0	120	1	0
West Adderbury Turn	33	24	68	37	25	44	10	0	0	241	1	0
Culham Hedge	0	22	18	0	9	40	20	0	0	109	0	0
Tackley Turn	0	4	224	0	8	82	0	0	0	318	10	0
Banbury-Warmington	13	28	33	7	23	29	0	0	0	133	1	0
Tackley Heath	1	13	67	0	11	67	0	0	0	159	5	0
Hedge nr. Tackley Turn	1	8	139	0	4	43	5	0	0	200	52	1
Eynsham Road	36	5	81	2	4	22	2	0	0	152	3	0
Easington	1	2	12	1	1	8	0	0	0	25	0	....
Near Wroxton	2	4	6	3	3	19	0	0	0	37	0	....
Edge Hill	4	2	10	0	0	1	0	0	0	17	0	....
Fyfield	29	4	26	22	11	59	0	0	0	151	3	0
Faringdon Road	3	21	61	0	4	23	0	0	0	112	7	0
East of Pusey Common Wood	2	0	6	2	0	8	0	0	0	18	0	....
Golden Butts	0	5	12	0	1	4	0	0	0	22	0	....
West of Pusey Common Wood	23	2	34	11	5	93	4	0	0	172	1	0
Oak Holt	0	15	38	3	9	34	0	0	0	99	0	0
Cumnor-Farmoor	2	5	72	0	1	32	22	0	0	134	2	2
Botley	1	0	37	0	0	4	15	0	0	57	6	0
Stretham	0	2	26	0	0	3	0	0	0	31	2	....
Kingston Hill	10	4	58	8	2	18	0	0	0	100	1	0
Parks Hedge	1	1	12	0	1	61	0	0	0	76	0	0
Canal Bank	17	25	72	7	27	120	9	1	1	279	10	0
Hinksey Hedge	5	2	11	4	2	10	0	0	0	34	1	....
Wytham Lane 1	2	1	13	1	0	5	0	0	1	23	1	....
Wytham Lane 2	3	0	23	0	0	17	11	0	0	54	7	0
Standlake	3	7	42	14	1	5	8	0	0	80	2	0
Woodstock Road	1	2	17	1	3	5	0	0	0	29	3	....
Hedge S. of Islip	3	12	33	4	9	22	4	0	0	87	1	0
Woodstock Rd. level crossing	8	6	14	0	0	0	0	0	0	28	0	....

In the Ballyness Bay collection there is a significant deficiency of unbanded albinos ($P < 0.01$). There is an association in the Thruxton collection but it is not possible to determine whether it is between albino and colour or albino and 00000 (P for pink vs. brown is < 0.01). The data from the Pentridge show that there is an association with colour ($P < 0.01$), and this is confirmed by the data from a separate collection from the Pentridge (Pentridge 2), which was not taken at random, the more brightly coloured shells being preferred.

But this preference merely raised the proportion of pink shells taken and therefore increased the probability of obtaining albino pinks if they were present. In fact, no albino pinks were found at all at this locality.

It appears from tables 2–6 that 00000 as against banding, but not 00300 as against other banded forms, is associated with all three colours. The association is too strong to be due to random sampling ($P < 0.001$). Absence of association in any colony does not mean absence of linkage: presence of apparent association in only one or two among a large number of colonies could arise from sampling errors. The data from colonies in Germany and Austria given by SCHILDER (1926) also indicate linkage between colour and 00000. The presence of these striking associations can be due only to exceedingly heavy selection, or to a moderate degree of linkage with selection, or to very close linkage indeed, or to multiple allelomorphism. Very heavy selection of the degree necessary to produce these striking associations without linkage is most unlikely. Multiple allelomorphism does not appear to be extensive. Albino

TABLE 5

Locality	Yellow			Pink			Brown			Total	Effectively unbanded except 00000 and 00300	00000 with traces in samples of more than 50
	00000	00300	Others	00000	00300	Others	00000	00300	Others			
Rough herbage												
Wittenham Clumps	13	3	177	6	3	75	2	0	0	279	3	0
Wittenham Clumps downland	5	0	14	0	0	4	0	0	0	23	0	....
Hinksey Hill	59	42	267	5	4	57	0	0	0	434	32	0
Southmoor	69	19	106	34	1	27	2	0	0	258	7	0
Bicester Road	30	32	50	0	5	18	14	0	0	149	2	0
Nettlepatch, Cumnor Hill	19	0	50	39	0	53	0	0	0	161	11	0
Southern Bypass	25	13	58	11	7	53	0	0	0	167	21	0
Attleborough	0	0	108	0	0	64	0	0	0	172	0	0
Cutslow Park	4	1	30	1	1	15	1	0	0	53	2	0
Aston Tirrold	6	0	9	7	0	23	20	0	1	66	8	2
Scolt Head	3	10	137	0	0	2	4	0	14	170	3	0
Rugby	58	63	53	17	20	12	0	0	0	223	0	0
Sheepstead Hurst	1	3	22	4	1	20	7	0	0	58	0	0
Eynsham Tollbridge	0	2	62	0	1	45	0	0	0	110	2	0
Cassington Halt	30	32	68	0	10	7	0	0	0	147	9	0
Northern Bypass	5	2	31	0	8	20	7	0	0	73	4	0
Hurst Rise Road	3	8	52	1	1	14	2	0	0	81	3	0
Chilswell Farm	4	2	12	0	0	3	0	0	0	21	1	....
Christmas Common downland	0	11	55	19	6	61	0	0	0	152	18	1
Pentridge 1	0	66	208	1	34	93	6	2	18	428	4	2
Pans Hill	0	8	18	0	30	63	0	0	0	119	2	0
Kennington Road	7	1	12	6	2	5	1	0	0	34	0	....

is clearly not an allelomorph of colour or banding; it is linked to banding and to colour. 00000 is associated with all three colours and has been shown by FISHER and DIVER (1934) to be linked with the pink-yellow locus. Brown could be an allelomorph of yellow and pink or a different gene converting either or both of the other colours to brown. If it be a separate gene, it is certainly linked with 00000, which itself is linked with the pink-yellow locus. If it converts only one of the other colours, the ratios of banding classes in the brown class should be the same as in either pink or yellow. The tables show clearly that this is not so. Brown must therefore be either an allelomorph at the pink-yellow locus or linked with it.

TABLE 6

Locality	Yellow			Pink			Brown			Total	Effectively unbanded except 00000 and 00300	00000 with traces in samples of more than 50
	00000	00300	Others	00000	00300	Others	00000	00300	Others			
Short turf												
Crowell Hill	0	0	32	13	0	95	0	0	0	140	12	0
Rockley 5	58	55	1	27	11	0	64	2	0	218	1	0
Rockley 7	7	7	1	4	3	0	11	1	0	34	1	....
Rough Down	119	35	12	7	23	13	93	16	6	324	12	7
Kimpton Down	0	1	12	18	20	15	10	9	9	94	1	2
Thruxton	0	0	0	2	115	10	24	5	0	156	2	2
Background unscorable												
East Ilsley	0	0	6	0	1	0	27	4	4	42	2	....
Rough Common, Wytham	12	7	37	20	12	85	13	0	0	186	14	0
Sowberry Court	2	0	9	15	0	27	36	0	0	89	0	14
Chute Windbreak	1	6	5	1	12	13	0	1	0	39	0	....
Pulpit Hill (Lower slope)	0	3	37	52	3	59	0	0	0	154	7	0
Cothill	0	0	16	5	1	11	0	0	0	33	3	....
Colonsay	0	3	33	0	1	35	0	0	0	72	0	0
Sliding Hill	6	3	17	27	6	43	0	0	0	102	1	1
Rockley 4	22	17	0	19	10	0	42	0	0	110	0	0
Rockley 3	18	12	0	22	4	0	21	0	0	77	0	1
Shepherd's Hey	1	0	31	13	0	21	5	0	0	71	2	0
Skegness	0	0	14	0	0	18	4	0	0	36	0	....

There is evidence that 00300 is at a different locus from 00000 (LAMOTTE 1951) and our data do not show that 00300 is associated with colour. Some of LAMOTTE's data for French colonies suggest linkage at the other loci.

It seems, then, that certainly three and probably five loci are involved in the production of the commonest variations, and that there are at least three very closely linked genes associated with the polymorphism. They are 00000, Albino and Pink together with their allelomorphs.

SELECTION

Several authors (HALDANE 1932; ROBSON and RICHARDS 1936; DIVER 1940; DOBZHANSKY 1941 but not 1951; HUXLEY 1942; MAYR 1942; CARTER 1951) have stated that variation in *C. nemoralis* is random; some have suggested that the differences between colonies or parts of colonies are very probably due to genetic drift. These conclusions rest upon an error of procedure (CAIN 1951a, b). Because a worker has been unable to correlate variation with any environmental or other factors, it does not follow that no correlations exist. In fact, the distribution of varieties in this species is controlled primarily by natural selection.

Selection by visual predation

Selection for both colour and banding has been directly demonstrated. SHEPPARD (1951) has shown that in Wytham Woods thrushes (*Turdus ericetorum*) do exert a visual selection while preying on these snails, and that the selection varies with seasonal changes in the background on which the snails live. When the woodland floor is brown with leaf-litter and exposed earth in early spring, yellow shells are at a disadvantage to brown or pink ones, but when in late spring the background becomes green, they are at an advantage. LAMOTTE (1951) has shown by the comparison of intact shells with shells broken by thrushes that in certain localities unbanded shells were at a disadvantage to five-banded ones. According to him, shells with 00300 or 00345 were intermediate in selective value but closer to the unbanded. We have investigated a colony of *C. nemoralis* in Marley Bog, a small hill-side fen, maintained by spring water, in Wytham Woods. The colony is predated by thrushes which are forced to carry the snails a few yards on to a bank above the fen where there are stones, in order to crack them. The thrushes were watched every day from July 4 to 20, 1951 by MR. J. A. GIBB, who very kindly collected the broken shells for us. Collections of live snails were made by us, taking all the snails discovered in an intensive search of a series of small patches of herbage: the composition of these is given in table 7. There was no evidence of selection for colour, which is accordingly disregarded in this table, from which a comparison of live and predated snails can be made. There is good evidence ($P < 0.02$) that unbanded shells 00000 are at a selective advantage to effectively banded ones. In previous papers (CAIN and SHEPPARD 1950; SHEPPARD 1952) we have suggested that since the lower bands are normally partially or completely hidden in the living snail, shells with bands 1 and 2 both absent can be considered as effectively unbanded phenotypically. LA-

TABLE 7

	Unbanded shells	Other effectively unbanded shells	Effectively banded shells	Totals
Living snails	153	143	264	560
Predated snails	204	173	486	863

MOTTE's data suggest that the varieties 00300 and 00345 may be intermediate in selective value between 00000 and 12345, as might be expected. At Marley Bog, the selective value of 00300 and 00345 (which with 00000 make up the class of effectively unbanded shells there) is so close to that of 00000 that the figures give no indication whatever of any difference, but do show a significant difference of these two combined from effectively banded shells ($P < 0.001$). Consequently these forms at Marley Bog are effectively unbanded. Since in both LAMOTTE's and our data these intermediate forms tend to resemble 00000 in selective value, it is justifiable to combine them with 00000 in a class of effectively unbanded as against effectively banded shells, a useful simplification. Direct evidence of selection thus supports a classification originally based on the appearance of the shells judged by the human eye.

Direct evidence of selection has so far been obtained in a few localities only, but is amply supported by indirect evidence drawn from a large number of colonies. We have investigated all the colonies we have found, and our sample of them is biased only in so far as we have looked for these snails in localities where the background could be classified (as beechwoods, downland, hedgerows etc.), avoiding those where there is a mixture of types of vegetable formations. The few colonies on mixed background that have been found are listed separately in table 6.

It was shown (CAIN and SHEPPARD 1950) that there is a strong correlation between the proportions of varieties in each colony and the characteristics of the exact background on which the snails are living. On the greener backgrounds there is a high proportion of yellow shells, on the more uniform a high proportion of effectively unbanded ones. This result is completely confirmed by more extensive collecting. The data for all our samples (except a few very small ones listed in CAIN and SHEPPARD 1950) are set out in tables 2–6 and a correlation diagram for percentage yellow shells, percentage effectively unbanded, and habitat is given in figure 1. The samples from the Pentridge, Scolt Head, Skegness, Ballyness Bay and Colonsay are omitted from the diagram, since we have not collected them personally nor seen their localities. In general, the classification by habitat gives a measure of the smoothness and greenness of the background (CAIN and SHEPPARD 1950). It will be seen that colonies in the same habitat-class tend to group together in the diagram (most closely in the least variable habitats). But it should also be noticed that even when the habitat classification is disregarded, there is an extremely good correlation between percent yellow and percent effectively unbanded. Because colour and banding are known to be genetically distinct, and there is no constant association of yellow with any particular banding-formula in individuals, this in itself can only mean that selection is operating. We have shown that this correlation is chiefly due to an association of colour and uniformity in the backgrounds we have studied, the browner ones being usually the more uniform.

In several of the colonies on mixed backgrounds, the background can be partially classified. Those at Sowberry Court and East Ilsley have already been discussed (CAIN and SHEPPARD 1950). Rough Common (Wytham) is partly mixed deciduous woodland and partly open grassland. The colony at Chute

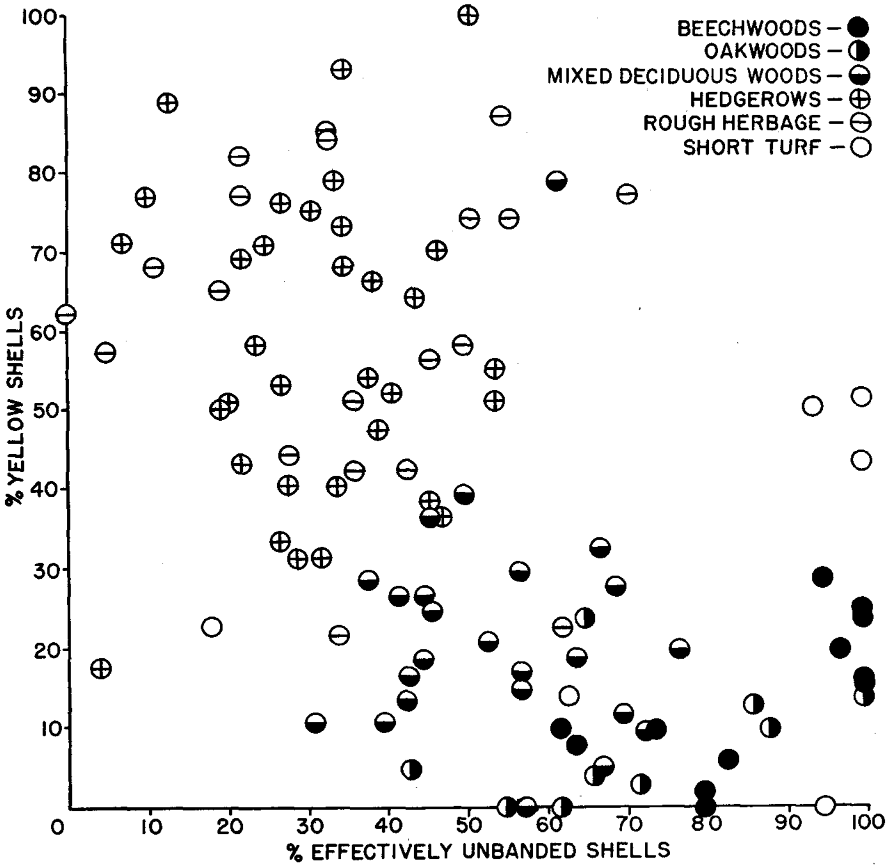

FIGURE 1.—Correlation-diagram, for % yellow shells, % effectively unbanded shells, and habitat, of all colonies of *Cepaea nemoralis* seen by us, except those with background unscorable.

windbreak was in a belt of beechwood 20 yards wide and in adjacent rough herbage. That at Pulpit Hill was on the lower slopes of a chalk escarpment, with scattered beech and oak trees, hawthorn and elder bushes, rough herbage, and patches of smooth green grass. In general the habitat approximates to woodland. Cothill comprises grassland, rough herbage and mixed deciduous woodland. The sample from Sliding Hill was from a mixture of habitats much as at Pulpit Hill but with ash instead of oak, and no hawthorn. Those from Rockley 3 and 4 are described by SHEPPARD (1952). That at Shepherd's Hey was from beechwood with much grass and a ditch full of wind-driven beech leaves bordered by a hedge of hawthorn with brambles. In all these colonies the proportions of varieties agree with their backgrounds taken as a whole. The localities most like woodland (Sowberry Court, Pulpit Hill, Sliding Hill, Shepherd's Hey) have colonies resembling those in the woodland classes, the others tending to be intermediate between the characteristics expected for the extreme types of habitat present.

Six colonies appear to have characteristics exceptional for the habitat class. Two, at Pan's Hill and Great Copse, Chislehampton, are in complete agreement with the backgrounds, which are exceptional in their habitat-classes. The colony at Pan's Hill is in a large thicket of rosebay willowherb merging with dense brambles. Although the habitat must be classified as rough herbage, the background at and just above ground level is brown, not green: correspondingly, the proportion of yellows is very low. Great Copse is an open elm wood on a hillside, with several springs, and the background at ground-level is of brilliant green short grass. The proportion of yellow is very high. Out of a total of 104 localities investigated by us personally, only four are really exceptional; these are at Crowell Hill, Aston Tirrold, Thruxton, and Kimpton Down, and, remarkably enough, they have many characters in common. All are on steep downland slopes with much grass, and a few bushes. All are infested by rabbits, and most of the shells collected were rabbit-predated. All have an unexpectedly low proportion of yellows, considering the greenness of the background, and at Crowell Hill, there is an unexpectedly high proportion of banded shells, much of the turf there being smooth and rabbit-grazed. All have a high population-density of *C. nemoralis.* The strong similarity of these four exceptional colonies indicates that there is some definite reason for their peculiarities other than mere random variation. It is possible (CAIN, in press) that rabbit predation by tone only, not colour and tone, is of particular importance in these four localities.

The similarity between colonies in similar habitats cannot possibly be due either to migration between adjacent colonies, or to geographical variation correlated with broad features of the environment such as climate. The colonies in each habitat-class are widely scattered in the region investigated, and their similarities are correlated only with the background, not at all with proximity. Figure 2 is a map of the Oxford district showing all the localities where colonies have been found. These colonies are isolated from one another by unsuitable habitats. It is obvious that colonies from mixed deciduous woodland agree in composition, although often separated and surrounded by colonies in rough herbage or hedgerows, which themselves agree within their habitat class, not according to their relative geographical positions. Geographical variation in the proportions of the shell-types tends to follow variation in the background very faithfully. At Rockley (SHEPPARD 1952) a single widespread colony occurs in downland and in three isolated beechwoods, separated by the downland. The different parts of the colony show a remarkable correlation with their backgrounds. A similar situation has been found at Tackley, north of Oxford, and Pusey Common Wood, ten miles west, where hedgerow colonies approach within a few feet of colonies in woodland without losing their distinctive characters (Pusey Common Wood and contiguous hedgerows on Oxford side and further side; Tackley Heath Wood, and Tackley Heath in tables 2, 3 and 4). That such situations can be found is the strongest possible evidence both for selection and for a very low degree of migration. LAMOTTE (1951) and SCHNETTER (1950) have found experimentally that migration is

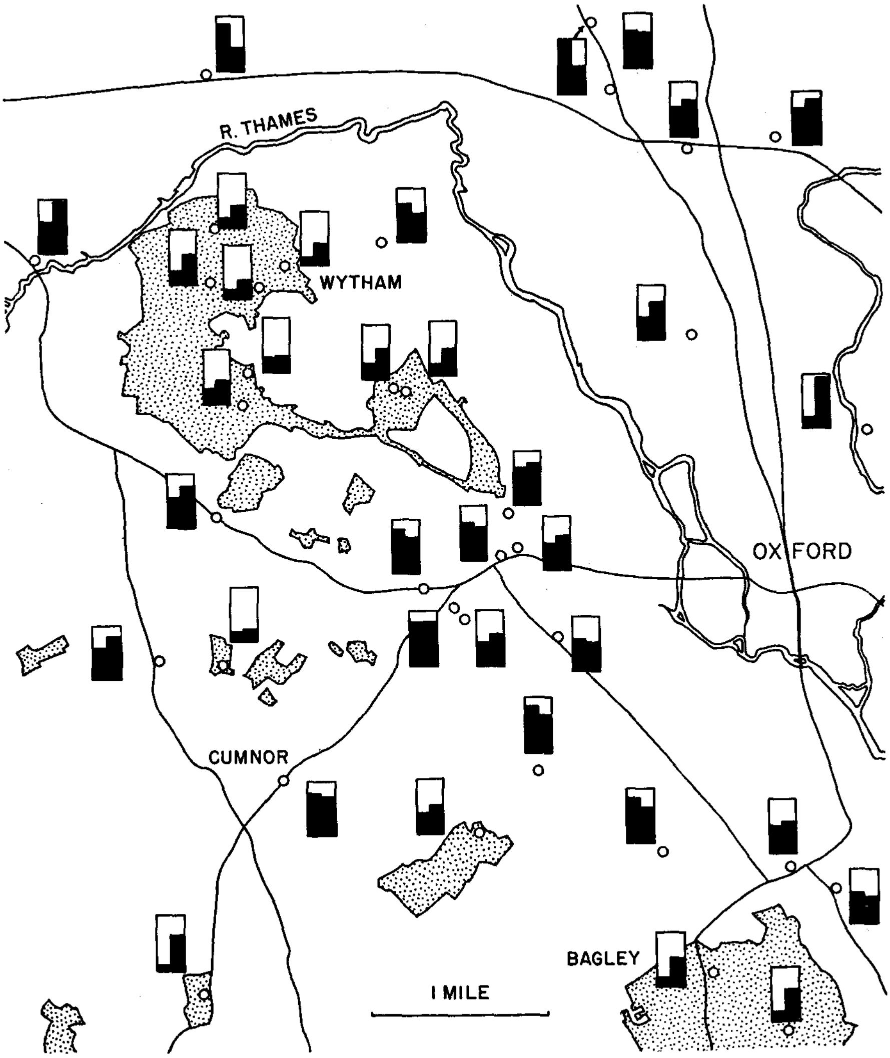

FIGURE 2.—Sketch-map of the Oxford district showing for each colony found % yellow shells (left hand column) and % effectively banded shells. Woodlands stippled; all colonies outside them are in hedgerows or rough herbage.

indeed very restricted. On the basis of his experiments, LAMOTTE concluded that no colony of more than 30 metres radius can be considered a panmictic unit, nor can linear colonies longer than 52.5 m. Both LAMOTTE, and SCHNETTER who obtained a rather higher value for the panmictic unit, used marked snails placed within a colony, and noted that they dispersed rather rapidly at first, becoming more sedentary later on. It is possible that if snails living in the colony had been marked individually and each immediately replaced where it was found, the estimate for the panmictic unit might have been even smaller.

Selection acts within as well as between the main banding and colour classes.

It has been shown (CAIN and SHEPPARD 1952) that not only the proportion of pinks and browns in a colony but also the shade of the pink shells is determined by selection, rich reds being found on beech leaf litter for example, but pale pinks and fawns on oak litter, which is a much paler brown. Selection also appears to act on the character *vestigial bands,* or traces. These appear only as small dark marks close to the lip in the normal band-position in the adult shell (p. 90). A shell with five traces may be genetically 12345, but phenotypically it is 00000. DR. LAMOTTE has very kindly informed us that in scoring his samples he counted all traces as full bands. We have ignored them as phenotypically of little importance. We find that the use of his system makes no important difference in the proportions of unbanded shells in our colonies; however, the data suggest that the unbanded individuals with traces are more abundant in woodlands than in hedgerows and rough herbage. This is to be expected, since the proportions of unbanded shells are low in these last two habitat classes, and banding is at an advantage. Consequently there will be selection against any modifiers causing banded shells to appear even partially unbanded. In woodlands, on the other hand, where unbanding appears to be at an advantage, such modifiers will be favoured. We have also noticed that in woodland colonies uninterrupted bands are often rather pale and narrow, while in hedgerows, even those contiguous with woodlands, the banding is usually more emphatic. These variations in breadth and intensity are difficult to score quantitatively.

Selection acts differently upon different combinations of shell characters. As already shown, the effects will be appreciable by examining wild populations only when there is strong linkage. Linkage between colour and unbanding, 00000, is sufficiently strong (p. 91) for these effects to be observed, and in fact it can be seen from tables 2–6 that yellow unbanded shells tend to be deficient in woodlands ($P < 0.01$) and to be in excess in some other habitats. An interesting exception is at Great Copse, Chislehampton where yellow 00000 is in excess, but the background here is, for a woodland, excessively green (p. 100). This variation in frequency of yellow unbanded shells is exactly what would be expected, as a result of visual selection in relation to the background, since when yellow is conspicuous as on brown backgrounds the plain yellow unbanded shells will be more obvious than those partly obliterated by banding. BOETTGER (1931) has already stated that unbanded yellow shells are never found in dense woodlands, and are common in open sunny places, but unfortunately does not give the necessary data. Our results support his view, although we do not usually find a complete absence of yellow unbanded shells in woodlands.

Visual selection acts not only on the shell but also on the rest of the visible phenotype. The colour of the snail's body varies from nearly white through grey to black, almost independently of shell colour and banding. The mean shade of the body-colour in each colony is strongly correlated with both the percentage of yellows in the colony (itself correlated with the greenness of the background) and with the exact shade of the pink shells (CAIN and

SHEPPARD 1952). The darker bodies, as might be expected, predominate on the darker backgrounds, and selection acts upon body colour although the body of the snail is far less often seen than the shell.

Non-visual selection

BOETTGER (1931) states, without giving details, that the degree of diversity in a colony is proportional to the diversity of its background. All our results agree entirely with this statement. On smooth uniform backgrounds such as beechwoods and short turf, the colonies are far less variable than in hedgerows, rough herbage, or even mixed deciduous woodland. Full details for some of the colonies investigated are given by CAIN and SHEPPARD (1950).

On uniform backgrounds, visual selection reduces the frequency of most of the varieties, and would be expected to remove them if the background remains constant. SHEPPARD (1951) has found that in Reserve Ride (Wytham Woods) of 1358 marked snails released on April 26th, 1950, 46 predated shells were actually found at thrush stones in the short period between 28th April and 5th June 1950. This indicates that about 3% of the population was predated in this period. At the beginning of the period, when the background was brown, yellow shells were at a disadvantage. His figures for selective destruction of yellows at the beginning of the period for three independent groups of shells are consistent and suggest that on the thrush-stones about 1.5 times as many yellows appeared as would be expected if predation was random. If the background were to remain constant (as it does in beechwoods and in many grassy places) then even with no more selective predation per year than that found in Reserve Ride between 26th April and 5th June 1950, it is clear that there would be selection against yellow shells on a brown background (or for them on a green one) of the order of 1% or more. This would remove either the yellows or the other colours from the colony relatively rapidly. A tentative estimate of population size at Marley Bog made by recapturing marked snails, gives about 10,000 adults present. From the degree of predation shown in table 7 between 4th July 1951 and 20th July 1951, it is obvious that selection for unbanded shells at this locality, with a constant background would be of at least the same intensity.

BOETTGER (1950b) and DIVER (1929) have pointed out that *C. nemoralis* has been polymorphic for banding at least since Neolithic times, and probably much longer. All its close relatives are polymorphic for banding and colour. Polymorphism in *C. nemoralis* must therefore be regarded as normal and stable. But it might be maintained either by selection for different varieties in different places, combined with gene-flow, or by mechanisms tending to maintain variability independent of the locality, such as that described by FISHER (1930a). The simplest situation is found when in a single pair of allelomorphs the heterozygote is at a selective advantage to both homozygotes. All the colonies we have investigated have been polymorphic, and of more than 800 colonies investigated by LAMOTTE (1951) only two are apparently monomorphic (yellow unbanded). To maintain polymorphism in all these colonies, many of which are well isolated geographically, migration must be frequent and widespread, unless visual selection is very low.

The remarkable correspondence found by us, of parts of colonies with their different backgrounds and the extensive experiments of LAMOTTE (1951) show that migration in *C. nemoralis* is very slight (except possibly by human aid in urban districts), and cannot maintain polymorphism in face of the high visual selection demonstrated by us. Therefore there must be some nonvisual selective pressure, of the type discussed by FISHER (1930a), which is stabilising the polymorphism.

There is good indirect evidence for nonvisual selection within the class of brown shells. We formerly considered (CAIN and SHEPPARD 1950) that there was some interference between brown and the expression of banding. Further experience in collecting shows that the faint fluctuations of ground colour simulating very weak banding in browns occur also in pinks and yellows, and that banding when it does occur in browns is as clear as in banded shells in the other colour classes in the same colony. As tables 2–6 show, banded browns are always far less common than unbanded ones. There is an excess over expectation of unbanded brown shells even if it be assumed that brown is an allelomorph of banding, not colour, and that the brown heterozygotes are unbanded and only the brown homozygotes are banded. This unlikely assumption much reduces the expected frequency for banded browns. Moreover, since the deficit of banded browns is independent of the background of each colony, and therefore of the direction of visual selection of banding, the assumption that brown is an allelomorph of banding leads to the conclusion that there is constant nonvisual selection against banded browns. If brown is not an allelomorph of banding but is closely linked to it, then again there must be selection constantly against banded browns irrespective of the background. No doubt visual selection will act on banded as against unbanded shells in brown as in the other colour classes. But since brown is by far the darkest of the general shell colours, and most like the bands in hue, it is to be expected that visual selective discrimination between banding classes in brown will be less than in any other colour-class. In fact, in this colour class only, it seems constantly unable to override the effects of nonvisual selection.

Direct evidence of nonvisual selection has not been recorded in *C. nemoralis*. SCHNETTER (1950) has shown very strong selection to be favouring yellow unbanded *C. hortensis* in a colony which he observed from 1942 to 1950. He finds that this variety is more abundant in drier and more open places, and correlates its increase with a drying out and clearing of the locality. However, thrushes feed in this colony, and it is possible that part of the increase may be due to visual selection. In *Fruticicola lanzi,* however, GAUSE and SMARAGDOVA (1940) have shown that there is a considerable difference between dextrals and sinistrals in their capacity to resist starvation.

MAINTENANCE OF THE VARIATION

Different authors have come to very different conclusions about the relative importance of selection, mutation, migration and genetic drift in maintaining the extraordinary variability of Cepaea. Boettger (1931, 1950a) considers that the degree of variation is controlled by the diversity of the background through visual selection, and that on uniform backgrounds the number of varieties will be reduced unless replenished by natural or artificial introductions. As Lamotte (1951) points out, Boettger has not published the data necessary to support his conclusions. Diver (1940) believes, on the contrary that variation in *C. nemoralis* is random, and that the difference between colonies is due to genetic drift, but his conclusions are equally unsupported by published evidence.

As just stated, Schnetter (1950) has found in *C. hortensis* evidence of strong selection which he correlates with a change in the environment. He did not investigate the relative importance of visual selection and climatic selection in detail but makes it clear that the nonvisual selection was the more important. He was unable to find evidence of similar selection in *C. nemoralis* living in the same area, but his investigations in the two species were not fully comparable since they differed very strongly in the proportion of varieties present. On evidence which, as he himself is careful to point out, is very inadequate, he believes that some geographical variation can be discerned in *C. hortensis,* not in *C. nemoralis,* and as widely separated colonies may be much more alike than nearly adjacent ones, he concludes that the overall influence of climatic selection must be very slight, and that a great deal of the variation between colonies is due to random extinction of genes (i.e., to genetic drift). This conclusion is entirely based on the assumption that the direction and intensity of selection cannot alter profoundly over short distances. Our results show that this assumption is incorrect (e.g., fig. 2).

Schilder (1950) has studied in considerable detail the colonies of *C. nemoralis* and *hortensis* on a small island off the north German coast. He mapped the distribution of each species and the occurrence of particular varieties, indicating for each collecting station the nature of the habitat (oak copse, cultivated land, etc.) and listing the principal plants present. He found that at certain stations, particular varieties were especially abundant, and that their frequencies tended to fall off rather uniformly with distance from these " centres." Both the ranges of the species and their geographical variation were quite different. Because he did not find these species in some apparently suitable localities, he considered that colonization of the island was still proceeding. Without giving a detailed analysis, he found no correspondence between habitat and the frequency of particular varieties. But he has not studied the appearance of the background in relation to local variation, and his floral data do not enable one to arrive at any estimate of it, since the same species of plant can produce very different backgrounds, depending on the density of individuals and their size. Schilder interprets these results as indicating that variation in these species is independent of the environment. He believes that it is maintained by introduction or mutation, the new forms spreading out from their place of origin in the colony by slow gene-flow. It is quite possible that colonization of this island is recent and still in progress, and that importations from outside are continuing. In this case, the colony is not in equilibrium with its environment, and one can draw no conclusions from an apparent absence of selection. But it should be noted that the variation-pattern observed by SCHILDER could be brought about in two ways. There could be either the introduction or local production of new forms in already colonized areas, or the introduction of one or a few individuals into unoccupied territories. In the first case, the new form cannot reach a high frequency at the place of origin in the face of continual gene-flow without a considerable selective advantage, yet that gene-flow is high seems demonstrated by the length and smoothness of the character-gradients claimed by SCHILDER. In the second case, local homogeneous populations will be produced. If these reach high population densities, and expand, they will eventually come into contact with other populations, interbreed, and produce clines, which will gradually disappear. Neither of these hypotheses is incompatible with the control of genes in the colonies primarily by selection.

In fact, gene-flow in these colonies is only inferred not demonstrated, since demonstration requires observations made at two separate periods, at least. But it is remarkable that all the unbanded *nemoralis* are pink, although yellows are present in other banding-classes. This can only mean that either there is strong selection (with linkage) against unbanded yellows, or that the unbanded allelomorph has not been on the island long enough for an appreciable frequency of the crossover class to appear. Even if there were absolute linkage (which is unlikely) one would still expect unbanded yellows to appear either by further introduction or by mutation, especially if LAMOTTE's estimate for this mutation rate in Cepaea can be believed (p. 107).

By far the most important single paper on Cepaea that has yet appeared is LAMOTTE's study of *C. nemoralis* (1951). This author's work on population-size, panmictic units, homogamy, and migration is the best yet produced. He is also the first to apply quantitatively SEWALL WRIGHT's equations for the interaction of selection, mutation, migration and population size to an ensemble of actual populations. His conclusions, based on a careful study of over 800 French colonies, are diametrically opposed to ours, since he believes that mutation assisted by migration is the prime agent maintaining the variation, that differences between colonies are due to genetic drift, and that selection, although present, plays an almost negligible part. In the colonies investigated by us, selection is the primary factor both in maintaining variation within a colony and in determining the differences between colonies. This apparent contradiction must be investigated.

LAMOTTE regards selection as unimportant for the following reasons.

(1) He finds no obvious correlation between variation in colonies and the environment.

(2) Although there is some selective predation by thrushes, these birds are only winter-visitors in France, and in winter most of their predation is non-selective.

(3) He can find no correlation whatever between variation in *C. nemoralis* and *C. hortensis* living together in the same place, on the same background.

(4) His data show that small colonies are more variable than larger ones.

(5) He has been able to fit to his data on the frequency of the gene for bandless in Aquitaine a curve derived from SEWALL WRIGHT's formulae, which indicates that in these colonies migration plus mutation is important and selection almost negligible. Using additional data from other areas he concludes that the mutation rate of the allelomorph for banding to bandless is 1×10^{-4}, and the reverse rate 5×10^{-4}, and that these mutation rates are sufficient to maintain polymorphism. He supposes therefore, that selection never plays more than an accessory part (1951, p. 230).

These reasons, and the conclusions based upon them, seem incorrect, on the following grounds respectively.

(1) Many of the localities investigated by LAMOTTE were, as he points out, in recently disturbed or unstable environments, and in these a correspondence of varietal proportions and the background is not to be expected. Also in many localities there was a mixture of habitats, such as we have avoided (p. 98, above) so that even if the proportions of phenotypes were controlled by visual selection, a correspondence could hardly be observed.

LAMOTTE makes no direct comparison of colonies with backgrounds, for reasons considered below. He does make comparisons of colonies classified by their broad habitats (1951, p. 135), but using such classes as " bottoms of valleys," " dry biotopes " and " sunny places " which are too broad to be useful in considering backgrounds or investigating nonvisual selection if visual selection is effective. However, he does use two classes, oak coppices, and hedges, which seem to be sufficiently homogeneous, and comparable to our classes, although as he gives no description of them it is not certain that several types may not be included. He considers only the proportion of unbanded to banded shells: a better estimate involves the proportions of effectively unbanded shells (p. 98, above) and of the various colour classes. His data indicate that variation between colonies in hedgerows is greater than in oak coppices, as might be expected. The mean frequency of unbanded shells, however, is higher in both classes than in our data, and is not significantly lower in hedgerows than in oak coppices. Since the backgrounds have not been described, no definite conclusion can be reached. It is quite possible that the observed higher frequencies of unbanded shells in his colonies could be due to climatic selection. SCHNETTER (1950) in *C. hortensis* finds that, largely as a result of nonvisual selection, unbanded shells are more common in open, dry, sunny places. LAMOTTE (p. 136) obtained indications of the same situation in *C. nemoralis*. Moreover, his data on climatic factors suggest that the highest frequency of unbanded shells occurs in regions where the July temperature is highest. As insolation is considerably higher in France than in Great Britain, a higher proportion of unbanded shells might be expected in France especially in the more open habitats such as hedgerows in contrast to woods.

LAMOTTE finds no evidence for broad climatic selection. However, to investigate this, he has combined all colonies in groups according to the values of particular climatic factors. If local selection of the type we have demonstrated is acting, then grouping the colonies by climatic characters alone will mask more or less completely the effects of climatic selection. Nevertheless his published results (p. 141) do suggest a correlation between the frequency of unbanded shells and temperatures in both July and January, but these two factors may not be independent. It is possible that if the effect of visual selection had been eliminated by considering only colonies on the same background, a significant correlation with climate could have been observed.

(2) In Britain the song thrush is certainly not the only bird that preys upon these snails (WITHERBY et al. 1943), and in Europe many birds are recorded as eating molluscs (KLEINER 1936, 1937). Half-grown individuals, in which colour and banding are well developed, could be eaten whole by many small birds, including, of course, thrushes, which need to bring only the larger individuals to the anvils. It is extremely unlikely that a scarcity of song thrushes in any district means the virtual absence of visual predators.

In about 40 of his colonies, LAMOTTE was able to obtain sufficiently large samples of shells broken by predators to make a comparison between them and intact shells. His illustration (p. 183) of shells broken by birds includes at least two which have every appearance of having been attacked not by birds but by mammals. (This conclusion has been very kindly confirmed for us by MR. D. J. MORRIS, who has made a special study of the subject, MORRIS, in press.) It is most unlikely that rodents and birds find the snails in the same way, so that combining all the predated shells in a colony may well obscure the effects of selection. Nevertheless, LAMOTTE has obtained evidence of visual selection in certain colonies, always against unbanded shells; in others he found no evidence of selection, although the snails were being attacked, and concluded that in these there was only nonselective winter predation by thrushes. He has not, however, excluded the possibility of important visual selection by other birds. He compared the proportions of unbanded shells in colonies with the presence or absence of visual selection, and found no correlation. But because selection can vary in intensity and direction, the average selective value of unbanded shells should be compared with their frequency in each colony. Only those colonies that have lived in the same habitat for a long period should be used, and to reduce the effects of nonvisual selection, comparison should be made only between those in the same sort of habitat and in the same area.

LAMOTTE has compared the diversity in frequency of unbanded shells in colonies known to be attacked by predators and in those he supposes to be exempt, and finds no difference. He comments on the high degree of diversity in both classes. But in fact, it is extremely likely that all these colonies are attacked by predators (many of which do not leave broken shells as evidence), and the high diversity is to be expected if visual selection is operative against a complicated mosaic of backgrounds, favouring unbanded shells on some and banded on others.

(3) Apart from all other considerations, LAMOTTE (1949, 1951) believes that it is possible to demonstrate conclusively that there is no selective in-

fluence of the environment upon the visible characters of the snail. The two very similar species *C. nemoralis* and *C. hortensis* are not infrequently found living together in the same colony. If visual selection is favouring a particular variety in one species in a mixed colony then it should favour it in the other species as well. Consequently there should be a correlation between the frequency of unbanded shells in *C. nemoralis* and *C. hortensis* in mixed colonies. LAMOTTE finds no trace of such a correlation (and neither do we).

But in fact such a correlation is not to be expected; and the stronger the visual selection the less likely it is to be found. With visual selection acting on phenotypes, the same banding patterns displayed on one ground-colour of the shell will not have the same selective values when on other shell-colours. In woodlands, where unbanded pink shells are at an advantage, there is nevertheless an excess of banding in the yellow as compared with the pink class in *C. nemoralis,* since the banding obscures the disadvantageous colour (p. 102, above). As yellow is far more common in *C. hortensis* than in *C. nemoralis,* one would expect to find—and one does find—that in *C. nemoralis,* unbanded pink shells are common in woodlands, but in *C. hortensis* banded yellows. On smooth green herbage, on the other hand, from the point of view of visual selection, a high proportion of unbanded shells would be expected in both species, so that there will not be a simple negative correlation.

TABLE 8

Locality	*C. nemoralis*						*C. hortensis*					
	Yellow		Pink		Brown		Yellow		Pink		Brown	
	Unbanded	Banded	Unbanded	Banded	Unbanded	Banded	Unbanded	Banded	Unbanded	Banded	Unbanded	Banded
Rockley 1, 2 & 3	37	33	77	12	74	4	1	35	0	0	0	0
Rockley 9	1	3	2	7	9	3	2	8	0	0	1	0
Ashbury	0	3	5	6	17	0	1	21	0	0	0	0
Beechgrove Farm Wood	0	5	31	16	7	0	2	13	0	0	0	0
Aston Rowant	0	0	23	7	0	0	0	3	0	0	8	0
Boarstall	0	0	54	79	0	0	2	16	0	0	16	1

Table 8 gives the proportions of banded and unbanded shells in both species in four mixed colonies investigated by us. Although there is a very striking correspondence between the background and the *C. nemoralis* population (see CAIN and SHEPPARD 1952; SHEPPARD 1952; and tables 2–6 in the present paper) there is little resemblance between the proportion of banded shells in the two species.

Furthermore, for a correlation to be apparent, the nonvisual selective values of the various allelomorphs (which SCHNETTER 1950 for unbanded *C. hortensis* found to be high and very susceptible to changes in habitat) must be nearly the same in both species, which is unlikely. Even if this were so, the correlation might be very feeble unless the two species were intermixed either on a uniform background, or at uniform density in each distinct area of an irregular background, and were predated in the same way and to approximately the same degree. SCHILDER (1950) finds that *C. hortensis* is much more addicted to sitting on stems and in bushes, while *C. nemoralis* is more usually found on the ground. This is in agreement with our own observations. DR. P. H. T. HARTLEY informs us that in his experience thrushes cannot effectively predate snails resting more than a few inches above the ground. Consequently even in the same habitat, the incidence of predation by thrushes on the two species is likely to be different.

(4) Recently LAMOTTE (1952) has claimed that the differences between small colonies of *C. nemoralis* are considerably greater than between large ones in respect of the frequency of the genes for pink, and especially for absence of bands. He considers that since the effects of selection are independent of population size, any difference in variance between large and small colonies must be due to random fluctuations (genetic drift). According to his data, within a limited region, drift is responsible for one half the variance between large colonies (3,000–10,000 individuals) and five sixths that of small ones (500–1000). This conclusion is unacceptable for two reasons.

(a) Because backgrounds vary considerably over small distances, and the larger colonies will tend to be spread over larger areas and therefore over more types of background than the smaller ones, it is to be expected that large colonies will tend to be more alike, since the diverse effects of selection in different parts of each colony will tend to cancel out when the colony is considered as a whole, and in any case will be reduced to a certain extent by gene flow. Small colonies will tend to be on more homogeneous backgrounds, and will therefore become more diverse by selection. If selection is acting in different directions in different habitats, as we have shown, then when gene frequencies for all the colonies (in many different habitats) within a region are combined and compared with those of other regions, there should be less variance between frequencies for regions than between individual colonies in the same region. LAMOTTE's figures show that this is so, and therefore fail to provide any distinction between the effects of diverse selection and of genetic drift.

(b) It is far from certain that the effects of visual selection are independent of population size. Thrushes at least (HARTLEY unpublished) and probably many other birds, take these snails especially at periods when other food is scarce, or when an unusually large supply of food is necessary (nesting period), and they appear to be able to find as many individuals as are required for food at any one time. There is no evidence whatever that they experience much difficulty in obtaining the snails. Consequently there is no reason to believe that the intensity of predation is the same in small and large populations. If each thrush tends to take as many snails as it requires, irrespective of the size of the population predated, then the intensity of predation and the effects of visual selection will be greater in the smaller populations.

If polymorphism in *C. nemoralis* is balanced, then the gene-frequencies will depart further from those obtained solely by the action of nonvisual selection in the smaller colonies. One cannot assume without proof that visual selection is independent of population size, especially when birds that hold territories are involved.

It is clear that before differences in variance between large and small colonies can be advanced as a proof of the importance of genetic drift, one must compare only colonies each of which lives on a single type of background, and show that the intensity of predation in them is irrespective of size.

(5) In view of his demonstration that selection is unimportant, LAMOTTE considers that the agreement between his data on population-size, migration and the frequency of the allelomorph for bandless, on the one hand, and a curve derived from SEWALL WRIGHT's equations·on the other, means that in this case the equations present an adequate analysis of the actual situation. Consequently they can be used to determine values for selection and the mutation rates, and to show how polymorphism is maintained. But this is so only if selection is very feeble, and as we have shown above, his conclusions on this point cannot be sustained. But if selection is important, then it is quite possible that the characteristics of the various backgrounds might be such that exactly the same curve could be produced by strong visual selection. In our colonies the effect of visual selection is obvious. Yet when a histogram for the frequency of unbanded shells is plotted (fig. 3a) it shows a remarkable resemblance to that obtained by LAMOTTE for the regions he investigated in the Pyrenees (1951, p. 131). However, when values for colonies in rough herbage and in hedgerows, on the one hand, and for all woodland colonies on the other are plotted separately, two obviously different curves are obtained (fig. 3b, c), the first of which is almost exactly like Lamotte's frequency histogram for the Parisian region (1951, p. 130) and the second resembles that for Aquitaine.

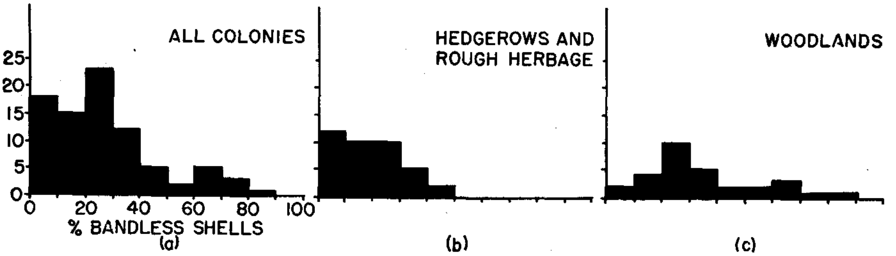

FIGURE 3.—Frequency histograms for % totally unbanded shells (as in LAMOTTE's diagrams) in colonies with samples of 50 or more. (a) All colonies; (b) hedgerows and rough herbage only; (c) woodlands only.

It is clear from these results that to combine the data from a particular region without regard to background is to obscure the effects of visual selection. It should also be noted that, as LAMOTTE has carefully pointed out, to construct the necessary curve for comparison one must assume both that selection is approximately constant throughout the region considered (1951, p. 202) and that the selection coefficients are very small, of the order of size of mutation rates (1951, pp. 212, 213).

LAMOTTE's results lead him to postulate mutation rates of the order of 10^{-4} to maintain variation in this species. These values are far higher than those normally obtained. But since his data are in no way incompatible with ours, it seems far more likely that in France as in England, selection is the primary agent maintaining the polymorphism and controlling the differences between colonies.

The maintenance of polymorphism by selection can be brought about by two principal methods (FISHER 1930a). Either the genotypes concerned become advantageous when rare and disadvantageous when common, or certain gene-combinations stand in particular ratios of selective advantage to others. In the simplest case, the heterozygote of a single pair of allelomorphs or for a chromosomal rearrangement is at an advantage over both homozygotes.

Although there is no evidence for the first method in Cepaea, it remains a possibility, in view of the work of DE RUITER (1952). This author has investigated certain birds preying on very protectively coloured insects, and has shown that when they encounter one of these they search for others of the same sort for some little time. If one can conclude from this that the finding of one form decreases for a time the chances of finding another, then it is possible that in such polymorphic species as *C. nemoralis,* the most abundant varieties will be relatively more heavily predated. The birds are most likely in searching for food to notice the more conspicuous and the commonest varieties. If the more conspicuous varieties are rare, then after a time, the search for further individuals of these sorts being unsuccessful, the birds will stop looking for them. The chances are that they will then be started on another hunt by encountering one of the more abundant varieties, and they will be able to hunt successfully for this phenotype for a much longer time. This will decrease the chances of their finding more of the rare conspicuous forms. There is no evidence for this in Cepaea, and, in our experience, one does not find on thrush stones an excess of one common variety on one day and of a different one on another day. Although the possibility is remote, it does indicate how slight differences in the methods of predation used by different predators may produce very different selective effects.

The great importance in *C. nemoralis* of the second method, namely selection favouring certain gene combinations, has already been fully demonstrated above (p. 104). All the available evidence points to its being the principal mechanism for maintaining polymorphism in this snail. Nonvisual selection of certain character-combinations involving more than one locus has already been demonstrated between brown and banding, as has visual selection involving other colours and banding (pp. 102, 104 above). Moreover, polymorphism may be considerable in banding even when only one colour is present. This fact indicates that its maintenance is due in part at least to the physiological advantage of heterozygotes at each locus.

It is remarkable (FISHER 1930b; HALDANE 1930) that the combination of (i) considerable and stable polymorphism, (ii) close linkage between many of the loci concerned, and (iii) rather frequent occurrence of a genotype recessive to most of the others involved in the polymorphism, is common to widely different groups of animals, and has nearly always been found when species highly polymorphic for visible characters have been investigated genetically. It occurs, for example, in *Cepaea nemoralis* and *C. hortensis* (Gastropoda), in Lebistes (Teleostei), and in several genera of Orthoptera (Apotettix, Paratettix, Chorthippus). In *C. nemoralis* we have shown that selection coefficients certainly greater than 1% are acting. FISHER (1930b, 1939) has remarked on the probability of high selective values in Lebistes, and in Paratettix and Apotettix has demonstrated values ranging from 6% to at least 40%.

FISHER (1930b) has given reasons for believing that the dominance relationships are a necessary consequence of the close linkage. FISHER and HALDANE agree that duplications and translocations may be the causes of close linkage. Translocations, however, tend to be disadvantageous and rare in nature. Duplications have been inferred in Orthoptera (WHITE 1945). In recent years it has been found that inversions are relatively abundant in wild populations (WHITE 1951; DOBZHANSKY 1951), that they are associated with stable polymorphism in Drosophila, at least (DOBZHANSKY 1951), and that they have very high selection coefficients. The very different linkage values for colour and banding in *C. nemoralis* reported by FISHER and DIVER (1934) strongly support the view that chromosomal rearrangements, probably inversions, are present in *C. nemoralis.*

EVOLUTIONARY SIGNIFICANCE OF THE VARIATION

The evolutionary significance of polymorphism in Cepaea and other forms is highly obscure. There is no evidence whatever that if every population of *C. nemoralis* were to become monomorphic overnight, the species would not continue to survive in the same places and at the same densities as before. Its local geographical distribution is probably determined primarily by the nature of the soil, and the sizes of its populations by this and density-dependent factors. Any slight increase in predation that might occur as a result of a change to monomorphism could easily be compensated by a change in the balance due to the density-dependent factors.

SCHNETTER (1950) has suggested that polymorphism in *C. nemoralis* is adaptive. As the different varieties have different selective values, a population might be enabled to persist through large climatic variations by changing the proportions of the different varieties and thereby maintaining its density of individuals. DOBZHANSKY (e.g., 1951) has suggested that balanced polymorphism in general is adaptive, both in promoting persistence of the species and in enabling a larger variety of niches to be exploited. But this hypothesis rests on the unlikely assumption that because one of two varieties is inferior to the other when in competition with it in the same population, it is normally incapable under the same environmental conditions of persisting as a pure population. Because yellow shells are at a disadvantage to others in beechwoods, it does not in the least follow that an entirely yellow population could not persist in a beechwood (in the absence of pinks). The relationships between the ecological factors that control the size of a population and the selective values of particular genotypes within it have never been adequately explored.

It would be very interesting to compare the density under different environmental conditions of breeding communities of Drosophila (in population cages) some of which are monomorphic for certain inversions and others polymorphic. DOBZHANSKY has suggested (1951, p. 123) that a population of *D. pseudoobscura* homozygous for the inversion ST is at a disadvantage under winter conditions. Exactly what is meant by a population being at a disadvantage is not certain. Presumably the population size is expected to decrease to a dangerously low level. This could be tested by the experiment suggested above. It will be rather surprising if any great difference in density between monomorphic and polymorphic populations is demonstrated.

As FISHER (1930a) has shown, whenever heterozygotes are at an advantage to both homozygotes, irrespective of the reasons for this advantage, stable polymorphism will result and persist, while if either homozygote has the highest advantage, only transient polymorphism will result. Consequently instances of stable polymorphism will accumulate, and will be frequently observed. Its widespread occurrence is evidence that it is maintained, once it has appeared, by selection, but not that it is, as such, of any *adaptive* value. Adaptation and selection are not synonymous, as has been clearly shown by FISHER (1930a), and SOMMERHOF (1950), and by CROSBY (1949) in the particular case of *Primula veris.*

SUMMARY

(1) The very variable European land snail *Cepaea nemoralis* has shown stable polymorphism since before the Neolithic period. The proportions of different varieties vary considerably from one colony to the next. It has been claimed that this situation is due to genetic drift.

(2) We have shown that this snail is subject to strong visual selection by birds, which results in a correlation between the varietal composition of each colony and the exact background on which it lives. This selection must be balanced by strong nonvisual selection, for the polymorphism to be maintained in each colony.

(3) The genetics of the variation is remarkably similar to that in other unrelated polymorphic species in which also high selective values have been demonstrated or inferred. Most of the loci investigated (at least 3 and probably 4) are linked, and one very frequent variety is recessive to all the other common ones (universal recessive). The degree of linkage varies, and it is probable that the loci concerned are associated with inversions.

(4) LAMOTTE (1951) after a very careful study of French colonies, has concluded that polymorphism is maintained by high rates of mutation (greater

than 10^{-4}) and that selection is negligible, also that the differences between colonies are due to genetic drift. These conclusions are shown to be unacceptable, since they are based on data grouped in such a way as to obscure the effects of visual selection, and depend on theoretical considerations involving the assumption that selection is negligible, which is invalid.

(5) Although polymorphism in this and other species is controlled by selection, there is no evidence that it is adaptive and contributes to the persistence or ecological expansion of the species. Theories of adaptive polymorphism rely on an unlikely assumption concerning the relations between factors controlling the density and persistence of populations on the one hand, and the relative selective values of alternative genotypes within them, on the other.

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