NATURAL SELECTION IN *CEPAEA* ON
PORTLAND BILL

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Received 24.v.67

1. INTRODUCTION

MUCH is known about the existence of balanced polymorphism in the genus *Cepaea* and the influence of bird predators in establishing a variety of equilibria under a wide diversity of environmental conditions. The Brown-lipped Snail (*C. nemoralis*) is particularly well suited for such investigations since it exhibits characteristic variations in the colour of the body, also in the background colour and degree of banding on the shell. Its near relative the White-lipped Snail (*C. hortensis*) is less variable, and with the exception of the work of Goodhart (1958) and Clarke (1962) has received comparatively scant attention. However, relative invariability is not necessarily a disadvantage and in the type of work we have carried out on Portland Bill, *C. hortensis* has proved to be an admirable species for study.

Collections of predated shells made at thrush stones revealed a discrepancy in the proportion of banded individuals compared with that of the adjoining population. Subsequent sampling showed this discrepancy to vary considerably from one locality to another at the same time of year, in an area of country where the surroundings are remarkably uniform both in their vegetation and topography. This strongly suggested the existence of area effects as described by Cain and Currey (1963). In 1962 we discovered the Strips locality (see below) where *C. hortensis* exhibits a characteristic morpho-ratio cline of banding which forms the principal subject of this paper. We selected this locality on account of the high density of snails and its close proximity to the Portland Bird Observatory. This greatly facilitated the problem of examining and marking shells in bad weather and also enabled us to obtain reliable records of the density of potential bird predators in the area throughout the year.

Although our studies have been mainly centred on *C. hortensis*, we have also a limited amount of data on *C. nemoralis*, thus enabling us to make certain comparisons of the two species in the same locality. Throughout, we have confined our attention to adult snails—those in which the lip of the shell has been developed.

2. THE STRIPS (PORTLAND BILL)

The area is situated about half a mile from the southerly tip of Portland Bill (fig. 1) and consists of a series of grassy banks about 400 yards long,

FIG. 1.—Map of the Strips locality and adjoining country.

varying in height from 2 to 6 feet and running parallel with one another in an E-W direction. The ground slopes gently downwards from north to south and from west to east (plate, fig. 1). The banks are separated by strips of cultivated land which vary somewhat in width but average about 7 yards wide. Oddly enough, little seems to be known about what must be an extremely ancient form of cultivation. Indeed, there is some evidence that

FIG. 2.—Vertical section through the geological strata of Portland.

the area may have been cultivated more or less in its present form since Saxon times. In the most recent review available (Drew, 1948) the suggestion is made that the strips represent the remnants of the mediaeval system of terraced open arable fields which were common all over England (but of which few examples remain) where the cultivated strips (lawns, as they are called locally) were separated not by hedges but by green banks of unploughed turf (balks). It is on these banks that *Cepaea* occurs (plate, fig. 1).

The geology of the area is, of course, well known, the local industry being the quarrying of stone (Arkell, 1947). The island of Portland is based on Jurassic limestone represented by the Lower Portland beds which provide

the famous building stone. Above these are the Lower Purbeck beds, followed by a layer of varied beach material, a further layer of shingle and gravel, and a course of about four feet of loam containing a considerable quantity of clay. Superficially, above the loam, is a layer known as the Head Layer composed of angular rubble from the Purbeck and Portland beds, interstratified with loam whose pH varies between 7.4 and 7.5 (fig. 2). Much of this rubble consists of limestone chips which vary in length from a foot to a few inches. These are used by birds for cracking *Cepaea* shells at the foot of each bank.

The vegetation of the strips is remarkably uniform, the banks being colonised predominantly by various species of grass mainly *Dactylis glomerata*, *Anisantha sterilis* and various species of *Festuca*, particularly *F. rubra*. Interspersed among the grass is a rank and somewhat ephemeral vegetation whose origin is not on the banks themselves but largely in the adjoining plough. This consists of plantains (mainly *Plantago lanceolata*), various Papilionaceae (mainly *Lotus corniculatus*), thistles (mainly *Carduus vulgare*), Hardhead (*Centaurea nigra*) and Bristly Ox-Tongue (*Picris echioides*). The banks are devoid of nettles, bramble and any form of tree. The crops cultivated in the areas between successive banks are mainly roots (e.g. turnips) and lucerne (*Medicago sativa*). Both species of *Cepaea* feed on a wide variety of vegetation but they have a decided preference for dead material, particularly the remains of *Carduus*, *Centaurea*, and *Picris*. This bears out similar observations made by Cain and others.

3. METHODS OF STUDY

(a) *Collecting procedure*

The effective sampling of snail populations depends greatly on the weather. Under the dry conditions which frequently prevail on Portland Bill as a result of the persistent wind, collecting can be exceedingly difficult. *Cepaea* retires to the depth of the grass stems and no amount of searching or scything will produce an appreciable number. But after rain or on mornings when there is dew, collecting is easy and in these favourable conditions it is often possible to obtain samples representing more than two-thirds of an entire population. As already pointed out, one of the advantages of Portland is that the bird observatory is only about 200 yards from the Strips locality. On every visit we have, therefore, aimed to collect each sampling area twice, once in the afternoon and again at first light the following morning. Comparisons of successive afternoon and morning samples from the same place show no significant difference between them, thus indicating that the behaviour of the various polymorphic forms is not subject to any sort of diurnal fluctuation. In general we have found early morning collecting far more satisfactory than any other method.

(b) *Marking*

At an early stage in our work we found it necessary to distinguish between the various snail colonies by marking, chiefly to study movement and bird predation, but also to gain a rough estimate of numbers from capture-recapture data. The snails were marked by removing a portion of periostracum in the vicinity of the umbilicus and applying a dot of quickly drying (dope) cellulose paint. A coloured patch on the ventral surface is

invisible to predators. We have no evidence to show how many paint marks get rubbed off but, judging by the numbers that needed touching-up even after two months' wear, it is clear that an appreciable proportion is lost. For this reason, if no other, estimates of numbers based on recaptured individuals are likely to be too large. The need to scrape off a patch of periostracum (which is often surprisingly hard) before marking, presents obvious problems in the field or where a source of main electricity is not available. To overcome this difficulty we have designed a portable shell-scraper. This consists of a 2-cell pocket torch in which a small Japanese electric motor (obtainable from toy shops) is inserted in place of the bulb holder. The motor is connected to the torch batteries and controlled by means of the torch switch. A small carborundum head (of the type used by dentists) is soldered on to the spindle of the motor. The apparatus has proved extremely efficient, the only precaution needed being to avoid drilling a hole in the shell. A pair of torch cells provides sufficient power to scrape at least 1000 snails.

(c) *Sampling areas*

Once we had suspected in 1962 the existence of a cline of banding along the length of each strip, it became necessary to select a number of sampling sites. These consisted of 50-yard stretches of bank (fig. 1). At first our attention was confined to a single bank (the third from that bordering the large field to the south), the sampling areas being designated A, B and C reading from east to west. Later (June 1963) we set up a second series of sampling sites along the next bank to the north, corresponding in position and extent to those already in existence on the neighbouring bank. Reading from east to west these were areas D, E and F (fig. 1). Within each area collecting was confined largely to the south face and top of the bank. On the north side the terracing had resulted in the level of the plough reaching almost to the top of the bank below. By selecting two comparable sets of sampling sites along neighbouring banks we hoped that it might prove possible to use one lot as a control should we wish to alter artificially the situation in the other—for instance, the gene-frequency at different points in the cline. The results we have obtained during the last few years have, indeed, enabled us to do this.

Although principally concerned with *C. hortensis*, we have also collected a certain amount of comparative data for *C. nemoralis* in the Strips area where it comprises about 8 per cent. of the *Cepaea* population.

4. DISTRIBUTION OF PHENOTYPES IN *C. hortensis*

(a) *Colour*

Like *C. nemoralis*, the colour of the shell in *C. hortensis* can be yellow, pink or brown. But from our experience on Portland Bill, it would seem that pink and brown are very rare, almost all shells having a yellow background (those on the Strips are exclusively yellow).

(b) *Banding*

The shell of *C. hortensis* may have up to five bands (very rarely six or more) which are usually dark brown and run along the whorls (fig. 3). Individuals occur fairly commonly, however, in which the bands are

translucent and unpigmented on a pale yellow or almost white ground-colour (var. *arenicola*, MacGillivray). To the human eye, from a distance of a few yards, these shells are almost indistinguishable from the normal, unbanded form. For scoring purposes, we have therefore followed convention (Cain and Sheppard, 1950; Clarke, 1960) and grouped together unbanded and *arenicola* into the category of "effectively unbanded".

When recording bands we have followed the practice established by Cain and Sheppard (1950) in *C. nemoralis*. These are numbered 1, 2, 3, 4 and 5 from the top of the whorl downwards (fig. 3). The absence of a band is indicated by 0 while fused bands are shown bracketed. Thus 023(45) describes a shell in which the first band is missing and the fourth and fifth

FIG. 3.—A shell of *C. hortensis* showing the arrangement of the bands and the convention used in numbering them.

are fused. Fusion is not regarded as complete unless adjacent bands are joined for at least 90° round the whorl from the lip. Variations in banding among *C. hortensis* on Portland are much less frequent than they are in *C. nemoralis*, the great majority having all bands present, 12345, with occasional fusions of 1 and 2, or 4 and 5 (or both). There is no doubt that, as Clarke has observed (1960), banded shells with fusions are slightly more obvious to the human eye than those without.

5. RESULTS OF SAMPLING (1962-65)

The full data are somewhat voluminous and can be obtained from the data depository of the British Museum (Natural History). In the interest of brevity we have included here only a summary with an accumulated total for each area (table 1). This procedure is not strictly justified on statistical grounds since some of the samples are heterogeneous judged by a χ^2 test, due to fluctuations in their size and the severity of selection. None the less, it has the advantage of simplifying rough comparisons. Where a more precise approach has been indicated, as when comparing the incidence of banding in one Area with that of another, we have applied the necessary statistical safeguards. In presenting the figures for banded shells we have shown only the commonest form with bands separate, 12345, and the most usual condition of fusion, 123(45). The remaining variants we have combined together under the general heading of "others". The condition

00300 which might well be regarded as "effectively unbanded" is almost unknown on the Strips. Throughout the whole of our collecting so far, we have encountered only one specimen. In determining morph frequency at different points along the two neighbouring banks, we have reduced our

TABLE 1

Summary of samples of C. hortensis from the Strips locality (1962-65)

Area	00000	<i>Arenicola</i>	Total effectively unbanded	12345	123(45)	Others banded	Total banded	Total	Percentage banded
A	2639	254	2893	538	64	90	692	3585	19.3
B	169	35	204	123	2	5	130	334	38.9
C	246	48	294	292	9	9	310	604	51.3
D	1288	171	1459	242	8	24	274	1733	15.8
E	274	47	321	137	2	3	142	463	30.7
F	264	72	336	330	5	9	344	680	50.6

analysis to the simplest possible terms—a comparison of "effectively unbanded" shells (consisting of unbanded + *arenicola*) with banded. All the *C. hortensis* shells collected so far in the Strips area have been yellow, and the number of banded individuals with one or more bands missing is relatively small (table 1). The proportions of "effectively unbanded" and banded

FIG. 4.—Distribution of samples of *C. hortensis* in relation to banding (1961-65). The scale shows the distance in yards.

shells thus provide a useful index for comparing the polymorphism existing in the three sampling areas along each bank (fig. 1). From the general pattern of morph frequencies it is clear that along each bank there exists a fairly steep cline, with the highest incidence of banding at the west end (fig. 4).

Samples from the ends of the same bank and from corresponding areas on adjacent banks were compared for the incidence of banding using χ^2

tests. The results are summarised in table 2 and show that the areas at the ends of both banks were markedly heterogeneous, while samples taken at corresponding positions along the two were similar. The heterogeneity in areas B and E in June 1964 was only to be expected from the number of samples examined. No data for area C have been included after June 1965, because on that occasion large numbers of unbanded individuals were introduced into the area for experiments, an account of which will be given in a subsequent paper.

Evidently the cline of banding is repeated in almost identical fashion along both Strips, there being strong evidence of homogeneity among samples obtained at the same time in corresponding collecting areas. For

TABLE 2
Summary of area comparisons 1962-1965

Sampling areas compared	Number of samples	Period	Probability range	Notes
A and C (South Bank)	9	Aug. 1962 to June 1965	$P = 0.01-0.001$	Samples in Aug. '64 and Oct. '64 too small to be significant.
D and F (North bank)	9	June 1963 to Oct. 1965	$P = 0.001$	Samples in Oct. '64 and Oct. '65 too small to be significant.
A (South) and D (North)	9	June 1963 to Oct. 1965	$P = 0.9-0.1$	
B (South) and E (North)	9	June 1963 to Oct. 1965	$P = 0.7-0.1$	Sample for June '64, $P = 0.05-0.02$.
C (South) and F (North)	7	June 1963 to June 1965	$P = 0.9-0.1$	Samples for Aug. '64 and Oct. '64 too small to be significant.

the purpose of lengthwise comparisons we are therefore justified in combining the two lots of samples. This accentuates the difference existing in the proportion of banded shells at the two ends of the banks. Moreover, the fact that the pattern of polymorphism in the Strips has remained substantially unchanged during four years of study points to a stabilisation between the inherent variation of *C. hortensis* and selective forces acting upon it.

Interesting evidence of the rapidity of colonisation by *C. hortensis* is provided from area A, in the whole of which the grass was accidentally burnt during October 1964, killing the entire population of snails. These we were able to collect after the fire, the shells being sufficiently undamaged for scoring. Even the paint marks were still clearly visible. By the following June the grass had recovered, and there were hardly any signs of damage other than charred earth. The colony of *C. hortensis* had already started to become re-established from the surrounding population with the proportion of banding at its former level. By August, numbers had increased considerably and still maintained the previous pattern of banding.

6. VISUAL SELECTION IN *C. hortensis*

During the period September 1961 to August 1964 we marked 6040 *C. hortensis*, using a different colour for each sampling area. Of these, 193 (3.2 per cent.) were found predated, 2.5 per cent. by birds and 0.7 per cent. by rodents. One of the most striking features of *C. hortensis* in Portland Bill

is the inadequacy of the concealment provided by all its phenotypes. To the human eye, banded and unbanded individuals are equally obvious (plate, fig. 2) and there is no reason to suppose that they appear any different to a predatory bird. Rodent predation usually takes place after dark and frequently when the snails are deep down in the vegetation, so the problem of concealment presumably does not arise. Bearing in mind the size of the snail population in the Strips (see Section 8) and the numbers of thrushes and rodents in the area at certain times of the year (see below), it is somewhat surprising that predation has not been more intense.

(a) *Bird predation*

Song Thrushes (*Turdus ericetorum*) are frequently seen to attack both species of *Cepaea* on Portland Bill. However, there are only two visual records of such predators on the Strips. Other occasional predators are Skylarks (*Alauda arvensis*) and Wheatears (*Oenanthe oenanthe*), but neither species has been observed feeding on snails in the Strips locality. The recovery of marked shells after predation, practically all of which are adults, suggests a distinctive behaviour pattern among bird predators which is confirmed by the two visual records. Out of nearly two hundred shells recovered, not one has been found outside the sampling area in which it was originally marked. Evidently the birds search for the snails, collect them from the vegetation and then crack them on the limestone chips at the foot of the bank (plate, fig. 3). Judging by our records over four years, predatory activity, as might be expected, reaches a maximum in the breeding season between June and August. Observations show that the number of birds likely to be in the vicinity of the Strips at any time depends greatly on the condition of the vegetation. On Portland, thrushes tend to congregate in bushes of bramble and sloe, both of which are absent from the Strips area. However, a wet spring followed by a warm summer such as occurred in 1962 and 1964, can result in a great outburst of rank vegetation which provides ample cover for birds. It is perhaps significant that the intensity of predation on *C. hortensis* was highest during these two years.

The resident thrush population on Portland is not dense, which is hardly surprising considering the bleakness of the surroundings and the widespread lack of cover. For most of the year numbers on the Bill total between 10 and 20 birds, but from September onwards, movements from the mainland and the Continent cause an increase which may reach a maximum of 100 or more by February. By April, when breeding begins, numbers have declined again, and the Bill usually supports a maximum of 10 breeding pairs (often less). There is no evidence from our records that other species of *Turdus* on migratory passage ever devour appreciable numbers of *C. hortensis* in the Strips.

Our records of predation during the years 1962-65 are summarised in table 3 together with estimates of the percentage of banded snails inhabiting the different sampling areas. The relationship between the proportion of banded shells available for selection and those actually predated in one area (A) is shown in fig. 5.

In presenting these data we have followed our previous practice (see table 1) of summarising the results for each area. Full details are available on request, as are those for predation by rodents (table 4).

In view of the cline of shell banding existing in the populations of

C. hortensis along the two neighbouring banks, we might have expected, if bird predation were a selective force, that selection against banding would have been differential at the high- and low-banded ends. In fact, our data suggest that this was not so, the lowest selection pressure against banding being in area A, itself a low-banded zone. However, as we have already stressed, the figures in table 3 are no more than summaries of heterogeneous data and a more rigorous analysis is necessary before any firm deductions can be made from them.

TABLE 3

Bird predation on C. hortensis in the Strips locality (1962-65)

Area	Effectively unbanded	Banded	Total	Percentage banded predated	Percentage banded living (derived from table 1)	Probability
A	550	167	717	23.3	19.3	0.01 > P > 0.001
B	55	53	108	49.1	38.9	0.8 > P > 0.7
C	62	96	158	60.8	51.3	0.01 > P > 0.001
D	73	26	99	26.3	15.8	0.5 > P > 0.3
E	41	28	69	40.6	30.7	0.05 > P > 0.02
F	38	48	86	55.8	50.6	0.3 > P > 0.2

In order to compare two series of related samples (*e.g.* living and predated snails) taken at the same times from the same area, we must first calculate the regression coefficient for each series. In effect, this gives us a measure of the slope of each graph, such as is illustrated in fig. 5. We can now compare pairs of regression coefficients by calculating the standard error of their difference. Using Student's test, the probability value of *t* can then be determined.

TABLE 4

Rodent predation on C. hortensis in the Strips locality (1962-64)

Area	Effectively unbanded	Banded	Total	Percentage banded predated	Percentage banded living (derived from table 1)	Probability
A	156	21	177	11.9	19.3	0.2 > P > 0.1
B	9	8	17	47.1	38.9	0.8 > P > 0.7
C	15	11	26	42.3	51.3	0.3 > P > 0.2
D	19	6	25	24.0	15.8	P > 0.9
E	2	2	4	50.0	30.7	0.7 > P > 0.5
F	5	3	8	37.5	50.6	0.7 > P > 0.5

The results of a comparison of bird predated and living snails (expressed as a probability) are shown in the right-hand column of table 3. It will be seen that the difference between them attained formal significance in three areas only (A, C and E). Moreover, in every area selection was against banded shells averaging about 8 per cent. overall. A striking feature of the data is their extraordinary inconsistency. Thus, while selection against banding attained a maximum (10.5 per cent.) in area D (a low-banded area) it was less than half this value (4.0 per cent.) in the comparable area A. Similarly in the high-banded area F, selection against banded was 5.2 per cent. compared with 9.5 per cent. in the corresponding area C, only a few yards away.

(b) *Rodent predation*

The difference between bird and rodent predated shells of *Cepaea* is usually easy to detect (Morris, 1954). While birds tend to concentrate almost entirely on adults, rodents frequently attack young snails—those in which the lip of the shell has not yet developed. The contents are removed by nibbling the region of the lip which is a great deal thinner in young shells. The rodent involved is not known, but rats seem by far the most

FIG. 5.—Relationship between living and predated banded *Cepaea hortensis* in area A. Data from samples 1962-65.

likely predators, since they abound among numerous dilapidated cliffside huts a few hundred yards away. Predation evidently follows a characteristic behaviour pattern. After seizing a snail, the rodent carries it along its run to a cache hollowed out in the depth of the grass. There, the snail is removed from its shell, devoured and the empty shell left behind. When looking for signs of rodent predation, therefore, it is a question of locating the runs and caches, both of which are hard to find. Unlike bird predation where our estimates are reasonably complete, figures for rodent predation are certainly too low and serve as no more than rough guides to fluctuating activity. It seems that the pattern of rodent predation is less seasonal than that of birds and it may take place at any time of the year. From table 4 it is clear that rodent selection of *C. hortensis* fluctuates even more than that of birds, ranging from a 7 per cent. selection against unbanded in area A to a roughly similar

pressure against banded in area D. The figures for probability in table 4 have been obtained from regression calculations similar to those used for bird predation. The fact that the difference between living and predated snails failed to reach a level of statistical significance in any area may well be due to the small numbers involved. The nearest approach is in area A, where the numbers of predated shells found were far greater than elsewhere.

7. MOVEMENT AND GENE-FLOW

Our sampling methods were designed primarily for the study of polymorphism, and they are ill adapted for the type of investigation carried out by Goodhart (1962) on movement in *C. nemoralis*. However, certain general conclusions of importance emerge as a result of the recovery of marked individuals.

(i) Movement of *C. hortensis* in the Strips locality is not confined to the banks but takes place equally readily across cultivated ground. Of 19 snails marked in one area and recovered in another, 7 had crossed from one bank to the next over about 7 yards of plough. Their average rate of movement was 7.4 yards per year. This must, of course, be a good deal faster than the average rate of movement for the whole population (estimated by Goodhart for *C. nemoralis* to be of the order of 3.3 yards per year).

(ii) From the few records of snails moving from one sampling area into another, both along the banks and between them, it appears that movement takes place in all directions. On Portland, activity ceases towards the end of October and begins again in April.

(iii) Our most extensive records are for area A, where out of 1297 snails marked between April 1962 and August 1964 some 62 (4.8 per cent.) were still in the area at the time of burning (October 1964). Fifty-three marked adults were eaten by birds during the period, thus reducing the total to 1244. If we assume a 50 per cent. annual mortality (Goodhart, 1962), we are left theoretically with about 230 marked snails by October 1964. In fact, only 62 remained, suggesting that about 170 had left the area (or lost their marks!). We recovered only 7 snails which had moved to other areas. Four crossed the plough to area D (see (i) above); the remaining 3 attained an average speed of 94 yards per year—surely approaching a maximum for *Cepaea* movement. The fact that a similar feat was recorded in another area suggests that such extensive wandering is by no means unique.

The general picture emerging is thus of a fluid population moving in every direction unimpeded by ecological barriers. Uninterrupted gene-flow along the length of the strips certainly occurs, but it takes place rather slowly.

8. SIZE OF *Cepaea hortensis* POPULATIONS

We have not found it possible to mount any very elaborate investigation of population size. An overriding consideration has been the number of visits that we have been able to make to Portland each year. The figures included in table 5 must therefore be regarded as approximations, but of the right order of magnitude. This is confirmed by calculations of the extent of bird predation based on the recovery of marked shells, which agree well with those derived from the estimates of population size (see Section 6a and Discussion).

They have been derived in four ways:

(i) In a few instances from mark, release and recapture. We have not pursued this method beyond the initial stage, since to introduce a system of re-marking would have vitiated the scheme we were using for other purposes. Numbers estimated in this way will tend to be overestimates due to the rubbing off of paint marks which undoubtedly occurred.

(ii) Subjective estimates based on the relative sizes of the samples collected in the six areas. The uniformity of the vegetation on the Strips has greatly facilitated collecting. On each visit we have invariably made two collections in each area, one in the afternoon and the other at first light the following morning. When conditions are ideal (with rain or a heavy

TABLE 5

Estimates of populations of C. hortensis in the sampling areas on the Strips (1962-65)

Date	Areas					
	A	B	C	D	E	F
Aug. 1962	1500 (b)	900 (c)	900 (c)	?	?	?
Oct. 1962	1000 (c)	800 (c)	600 (a)	?	?	?
June 1963	800 (b)	600 (c)	500 (c)	1500 (c)	600 (b)	600 (c)
Aug. 1963	700 (b)	500 (a)	500 (b)	1500 (a)	600 (a)	600 (a)
Oct. 1963	700 (b)	400 (a)	400 (b)	1800 (a)	400 (a)	1400 (b)
June 1964	500 (b)	400 (b)	500 (b)	1900 (b)	500 (b)	1600 (b)
Oct. 1964	300 (d)	?	?	?	?	?
June 1965	100 (b)	?	750 (b)	2000 (b)	500 (b)	1800 (b)

(a) = Derived from mark, release and recapture data.

(b) = Subjective estimate based on relative sizes of samples collected.

(c) = Guess, based on other estimates.

(d) = Total population (area burnt and all snails killed).

dew) on both occasions we believe it is possible to collect about two thirds of the total population. When the situation is favourable on one occasion only (either afternoon or morning) we have estimated our collections at about half the population. Under less good conditions our samples will have ranged from a third of the population to far less. When making estimates in this way, various other factors must be taken into account. For instance, when collecting conditions were adverse, we tended to concentrate on the extremities of each bank (areas A, C, D and F) since these showed the greatest divergence in banding (table 1). Moreover, in spite of their uniformity, not all the areas are equally easy to collect. Thus, while area D has a high bank and the snails are easily visible, area E has a much lower one and many *Cepaea* are difficult to detect when viewed from above. Had we spent the same amount of time searching each locality our samples would still not have been strictly comparable in terms of density. Such considerations have made the estimating of population size more complicated than appears at first sight.

(iii) By means of an informed guess based on other estimates and the general trend of numbers.

(iv) From an actual count of the whole population. This has occurred only once (area A in October 1964) when the grass was accidentally burnt and the whole snail population destroyed. The shells were collected after the fire relatively undamaged.

The value of the figures shown in table 5 lies chiefly in the comparison they provide of *Cepaea* densities in different areas on the two banks. However, a few other points of interest also emerge. The marked reduction in the populations of areas A, B and C towards the end of 1962 was almost certainly the result of temporary grazing by a herd of cattle coupled with severe drought in the late summer and autumn. Sampling of areas D, E and F had not yet started, so we have no comparable estimates of their populations during this period. In area A, following total destruction by fire in October 1964, the population had already reached a third of its former size by the following June—an interesting commentary on the extent of movement in *C. hortensis*. The general trend in population size appears to have been towards a reduction in the numbers along the south bank (areas A, B and C) and an increase in those of the north (areas D, E and F). Increases were particularly evident in areas D and F, but there is nothing to suggest why they should have occurred in these localities and not in others. Reference to tables 3 and 4 suggests that predation both by birds and rodents must have had relatively little effect on population size during the four years under review.

9. PERIPHERAL POPULATIONS OF *Cepaea hortensis*

In assessing the influence of selective agents on *C. hortensis* inhabiting the Strips, it was important to determine the extent to which the locality is isolated from neighbouring populations. Could it be, for instance, that the incidence of high banding at the west end and lower banding in the east was due merely to the influx of snails from adjacent localities subject to differing area effects?

The Strips locality is bounded to the north, south and east by agricultural land all of which is intensively cultivated and subject to regular ploughing

TABLE 6

Samples of C. hortensis from areas 1 and 2 compared with those from areas A and D (1966)

Area	Date	Total effectively unbanded	Total banded	Total
1 (SE)	June 1966	73	23	96
2 (NE)	June 1966	65	18	83
A	Aug. 1966	85	13	98
D	Aug. 1966	128	31	159

(fig. 1). There is, therefore, no possibility of colonisation from these directions. At the eastern end of the Strips the two sampling areas (A and D) are located some 25 yards from the extremity. In June 1966 we therefore selected two further localities at the extreme south-east (area 1) and north-east (area 2) in order to determine the nature of the *C. hortensis* populations available to colonise the Strips by moving westwards (table 6). The extremely dry conditions during June prevented adequate sampling of areas A and D, so this had to be done during August instead.

Comparison of the samples from areas 1 and 2 shows them to be homogeneous ($\chi^2_{(1)} = 0.34$; $0.7 > P > 0.5$), as also are those from areas A and D ($\chi^2_{(1)} = 1.25$; $0.3 > P > 0.2$). Combining the samples from areas 1 and 2

also those from areas A and D and comparing them gives $\chi^2_{(1)} = 1.90$; $0.2 > P > 0.1$. Evidently, we are justified in assuming the snail population at the east of the area to be homogeneous in respect of banding (between 20 and 30 per cent. banded shells).

At the western end of the area the situation is different, for here there is more or less uninterrupted continuity between the Strips and the surrounding downland. Accordingly, we set up five sampling areas (see fig. 1), two to the west of the road—area 3 (SW) and area 4 (NW); two to the east of the road—area 3A (S Intermediate) and area 4A (N Intermediate); and one (area 3B) extending between area 3A and the western extremity of area F. The results of sampling during June and August 1966 are summarised in table 7.

TABLE 7

Samples of C. hortensis from the western vicinity of the Strips compared with area F (1966)

Area	Date	Total effectively unbanded	Total banded	Total
4 (NW)	June 1966	145	14	159
4 (NW)	Aug. 1966	70	8	78
3 (SW)	June 1966	175	26	201
3 (SW)	Aug. 1966	87	9	96
4A (N Intermediate)	June 1966	37	2	39
3A (S Intermediate)	June 1966	26	4	30
3A (S Intermediate)	Aug. 1966	29	3	32
3B	Aug. 1966	17	6	23
F	Aug. 1966	78	53	131

The two samples from area 4 are obviously homogeneous as are those from area 3 ($\chi^2_{(1)} = 0.49$; $0.5 > P > 0.3$). Moreover, comparison of the two sets of samples combined gives $\chi^2_{(1)} = 0.62$; $0.5 > P > 0.3$. Evidently, at the western extremity of the Strips area where it merges with the adjacent downland, there exists a homogeneous population of *C. hortensis* with a banded morph frequency of approximately 10 per cent. As the population approaches the Strips a marked reduction in density occurs, although the frequency of banding remains the same and in marked contrast to that of area F where banded shells are about four times commoner. Thus, a comparison of the combined August samples from areas 3 and 4 with that from area F gives $\chi^2_{(1)} = 3.81$; $0.05 > P > 0.02$. We attempted to obtain a sample from the locality connecting the east end of area 3A with the beginning of area F (area 3B, see table 7). However, the density proved to be even lower there than in the adjoining area (3A) and, under unfavourable collecting conditions, we were only able to find 23 *C. hortensis* (26.1 per cent. banded).

The pattern of populations peripheral to the Strips thus appears to be as follows. To the east banding remains much the same as in areas A and D with a possible slight tendency to increase. Immigration to the Strips from the north, south and east is prevented by tracts of agricultural land. To the west there exists a large homogeneous population of *C. hortensis* about 10 per cent. being banded. This extends to within 35 yards of the western extremity of areas C and F while differing markedly from them (the incidence of banding in area F being about 40 per cent.). In the intervening

zone the population is very sparse but available evidence suggests that within this region there is a steep cline, the level of banding at the east end being about four times that at the west.

10. *Cepaea nemoralis* IN THE STRIPS AREA

While *C. hortensis* is the predominant snail in the Strips locality, *C. nemoralis* comprises roughly 8 per cent. of the *Cepaea* population. We have collected samples of *nemoralis* in areas A to F from August 1963 onwards and these are summarised in table 8. Since the numbers are small, we have made no attempt to subdivide the snails into different categories of banding. Moreover, we have followed the convention of classifying 00300 shells as effectively unbanded. We have not recorded predation on *C. nemoralis* since this amounts to no more than an occasional shell attacked by birds and none eaten by rodents.

TABLE 8
Summary of data for *C. nemoralis* (1963-65)

Area	Yellow				Pink			
	Effectively unbanded	Banded	Total	Percentage banded	Effectively unbanded	Banded	Total	Percentage banded
A	13	69	82	84.2	3	14	17	82.4
B	0	27	27	100	0	6	6	100
C	6	55	61	90.2	0	26	26	100
D	12	71	83	85.5	2	24	26	92.3
E	0	17	17	100	1	3	4	75.0
F	1	47	48	97.9	0	15	15	100

Analysis of the data for living snails presents some difficulty on account of the small size of individual samples. The only practicable course is to disregard seasonal fluctuations and to combine the samples for each area as a single total (table 8) also the totals for corresponding areas (A + D; B + E; C + F). Even so, information for the middle zone (B + E) is still deficient and provides little reliable evidence, other than that the snail populations in this region are predominantly banded. We can, however, compare the populations at the extremities of the Strips.

The data for areas A + D show the incidence of banding to be similar in both yellow and pink coloured shells ($\chi^2_{(1)} = 0.117$; $0.8 > P > 0.7$) so we are justified in combining the two totals for a comparison with areas C + F. Here a zero value for pink, unbanded shells necessitates the calculation of the exact χ^2 for comparison with yellow. This gives a probability of 0.81, showing that we are justified in combining the two totals and that the homogeneity which characterises the east end of the Strips also holds good at the west end as well. A comparison of the two ends in respect of banding gives $\chi^2_{(1)} = 7.93$; $0.01 > P > 0.001$, indicating a clear difference between them, 86 per cent. of the shells at the east end (A + D) being banded and 95 per cent. at the west end (C + F). Two interesting points thus emerge from this limited study of the two *Cepaea* species—that the incidence of banding in *C. nemoralis* is considerably higher than might have been expected in an area of such uniform grassland, and that variation in the proportion of banded shells in *C. nemoralis* and *C. hortensis* seems to follow a similar pattern, increasing along the length of each strip from east to west.

11. DISCUSSION

Cain and Currey (1963) have drawn attention to the steep clines of banding in *C. nemoralis*. Our studies in the Strips area of Portland show that a similar situation can obtain in *C. hortensis*, even under apparently uniform environmental conditions. An additional feature of the Portland populations has been the stability of their morph-ratios over a period of four years. This suggests the action of powerful selective forces, a view which is enhanced from a topographical study of the Strips. The locality is effectively isolated from neighbouring snail populations to the north, south and east (fig. 1). On the west side a dense population of *hortensis* inhabits the adjacent downland, with uninterrupted access to the Strips. Here the frequency of banding is about 10 per cent.—roughly half that of area A and four times that of area F. To offset the effects of gene-flow from the west into the high banded areas, we would have expected some indication of strong selection against unbanded individuals in areas C and F; but there was none. Further evidence of the magnitude of the forces involved in stabilising morph frequency in *C. hortensis* along the length of the Strips, derives from the fact that the cline is maintained in the face of an appreciable gene-flow along the banks in both directions, also between them. Although we have obtained no precise measurement of the average amount of movement in the snail population, the fact that exceptionally, individuals are capable of moving up to 94 yards in a year (the average is probably nearer 7 yards per year) suggests that this must be appreciable.

There remains the difficult matter of pin-pointing the selective agents responsible for maintaining a situation such as we have encountered on Portland. Our study of bird predation has been somewhat hampered by the fact that we still do not know for certain which species habitually feed on *C. hortensis*. If we assume that the bulk of predation is due to the song thrush (*Turdus ericetorum*) then, the fact that the number of birds in the area throughout the greater part of the year seldom exceeds 20, would explain the low level of predation observed. For 1963-65 this averaged about 4.2 per cent. of the total population per year. The figure of 12.8 per cent. in 1962 for areas A, B and C combined appears to have been exceptional. The data for rodent predation are less reliable but suggest an annual average of about 1 per cent., the maximum recorded being 3.1 per cent. in area A during 1962. These figures, based on our estimates of the population size, agree quite well with those derived exclusively from evidence provided by marked individuals (see Section 6).

Birds exerted a consistent selection pressure against banded morphs (average about 8 per cent.) in all Areas irrespective of whether their populations were high or low banded. Selection by rodents, as we might expect, was more erratic and shows no consistent trends. In the low-banded area A selection was against unbanded shells (8 per cent.), while in the corresponding area D the situation was reversed. In the high-banded areas C and F an excess of unbanded shells was eaten (3 per cent. in area C) but the records for area F are too few to be reliable. Had either of these agents played an appreciable part in maintaining the cline of banding in the *hortensis* populations inhabiting the banks, we would have expected some evidence of differential selection along their length. Such evidence has not been forthcoming.

Clarke (1962) has revived the interesting suggestion due to de Ruiter

that animals predating a polymorphic population such as that of *C. hortensis* may become conditioned to the commoner phenotypes and therefore tend to neglect the rarer ones, assuming that the common form is sufficiently distinct (as it undoubtedly is at Portland). Selective advantage might then vary inversely with frequency hence maintaining the polymorphic state. This certainly seems to be a plausible suggestion but there is no indication from our findings that the principle applies in the Strips.

Valuable information relating to possible selective forces involved in maintaining a cline of banding might be obtainable from a study of dead, unpredated shells. Unfortunately, these nearly always sink down into the dense mat of roots and litter at the base of the grass stems where they are difficult to find. Another line of inquiry which we are now pursuing concerns the incidence of banding in immature individuals. Such limited evidence as we possess suggests that this may differ appreciably from that of adults with still further selection against banded morphs.

The suggestion made by Lamotte (1959) that physiological selection can occur through the action of a gradient of climatic factors seems to us to provide the most likely explanation of the situation in *C. hortensis* that we have studied on Portland. While specific evidence of environmental variation along the length of the Strips is at present lacking, the fact that the fields where the banks occur slope downwards in a characteristic manner, both from north to south and from west to east, suggests that localised variations in temperature and humidity could occur. So far, our only detailed measurements of the environment have concerned the pH of the top soil which appears to remain nearly constant throughout the area.

Biologists now possess an immense amount of data covering a wide range of animals (and plants) showing that gene systems having distinct physical effects also influence physiology. Cain and Currey (1963) have provided field evidence of this in *Cepaea*. As long ago as 1940, Gause and Smaragdova investigating the significance of torsion in the Gastropod *Fruticicola lanzii* showed that dextral individuals survive conditions of starvation better than do sinistral. Evidently there is a wide field open for comparable laboratory studies in *C. nemoralis* and *hortensis* in order to determine more precisely any physiological effects of super-genes such as those controlling shell colour and banding.

An experiment which could throw some light not only on the severity of selection, but possibly on the nature of the agents involved, consists in swamping a high-banded area with unbanded snails and *vice versa*. This has now been set up, but present indications are that several years must elapse before results are available.

When comparing the distribution of the polymorphic forms in *C. hortensis* and *C. nemoralis*, Clarke (1960) and others have pointed out that, while the super-genes controlling polymorphism in the two species are probably homologous, the animals respond to the influence of their surroundings in different ways. It is of interest to find from the limited data available, that in the Strips area the pattern of banding in *C. nemoralis* appears to follow that of *C. hortensis*. Moreover, the comparison between the two species is rendered more valid by the fact that brown shells are absent in *C. nemoralis* and therefore not to be confused by potential predators with fused, banded shells of *C. hortensis*.

Plate I

- FIG. 1.—The Strips viewed from the western extremity of areas C and F. The field on the right is ploughed and forms the southern boundary of the locality.
- FIG. 2.—Banded, unbanded and var. *arenicola* (lowest middle) forms of *C. hortensis* in their natural environment. To the human eye, all appear equally visible.
- FIG. 3.—Bird-predated shells of *Cepaea hortensis* and *Helix aspersa* lying among limestone chips at the foot of a bank.

12. SUMMARY

(i) Two neighbouring populations of the polymorphic snail *Cepaea hortensis* have been studied in a restricted locality (the Strips) on Portland, Dorset. This consists of two parallel banks, being part of a mediaeval agricultural system. The closely related species *C. nemoralis* constitutes about 8 per cent. of the combined population of snails.

(ii) Sampling and marking of the snails have been carried out for a period of four years.

(iii) It has been established in *C. hortensis* that a cline of shell banding exists in the population ranging from about 20 per cent. at one end of each bank to roughly 55 per cent. banded at the other. The distribution of banding in the two banks is identical.

(iv) Data have been obtained for predation on *C. hortensis* by birds and mammals. These indicate that both the intensity of selection and its pattern are inadequate to account for the establishment or the maintenance of a cline of banding.

(v) Evidence derived from peripheral populations shows the Strips to be ecologically isolated except at the west end. Variations in the incidence of banding cannot be attributed to immigration and must be due to the action of selection.

(vi) The most likely explanation of the cline seems to be that the gene systems controlling shell banding also exert important physiological effects enabling the animals to adjust to a gradient of environmental variation. At present evidence for such variation is only indirect.

(vii) Information derived from marking experiments provides an estimate of the maximum rate of movement per year in *C. hortensis* and hence of the potential rate of gene-flow along the banks and between them.

(viii) The sizes of the various populations sampled have been estimated. This has enabled independent assessments to be made of the level of predation by birds and rodents as a check on the information derived from marking.

(ix) There is limited evidence for a cline of shell banding in *C. nemoralis*, similar to that in *C. hortensis* and operating in the same direction.

Acknowledgements.—It is a pleasure to record our gratitude to a number of organisations and individuals who have helped us with this work. To Mr F. R. Clifton, Warden of Portland Bird Observatory and Field Centre, we are grateful for providing excellent laboratory facilities and accommodation. Professor E. B. Ford, F.R.S., Professor P. M. Sheppard, F.R.S., Dr E. R. Creed and Mr K. G. McWhirter have kindly read the typescript and made many helpful comments and suggestions. Our thanks are also due to Mr W. M. M. Baron who identified the grasses, to Mr J. H. Durran for help with the regression calculations, and to Miss Christine Court who drew the figures. In collecting the numerous *Cepaea* samples, we have received valuable help from Mr A. Darlington, Mrs M. R. Dowdeswell and Mr E. C. Dowdeswell. Mr R. N. R. Peers, Secretary of the Dorset Natural History and Archaeological Society, and Mr R. Douch of Southampton University have provided us with much useful information on the historical aspects of the Strip system on Portland. One of us (W. H. D.) received a research grant and the loan of a calculating machine from the Royal Society, both of which are most gratefully acknowledged.

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