AREA EFFECTS IN *CEPAEA*

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[Plate 1]

CONTENTS

The snails *Cepaea nemoralis* and *C. hortensis* are remarkable for an extensive and stable polymorphism involving the colour and banding of the shell. It was formerly thought that the variation in frequency of the different morphs between populations was random. Cain & Sheppard, for *C. nemoralis* and Clarke, for *C. hortensis*, have shown that in many English colonies visual selection by thrushes, and no doubt other predators, strongly influences the frequencies of the morphs, the more conspicuous on a given background being more heavily predated. In consequence populations tend to match their backgrounds, but remain polymorphic.

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In some districts of high chalk downland, this correspondence with background does not occur. The predominance of a few morphs irrespective of habitat and background characterizes areas vastly larger than that of a panmictic population. Such a constancy of morph frequencies over a large and diverse area in spite of visual selection we call an *area effect*.

The principal district we have studied is the Marlborough Downs, where in an area of several square kilometres there are no five-banded *C. nemoralis* although in a contiguous area they predominate. Part of the non-five-banded area has a vast excess of browns, and another part of yellows. The form spread-banded and the cross-product ratio of pink and yellow to unbanded and banded also show such effects. In some places the morph frequencies change with extraordinary abruptness over 100 to 300 m. The area effects are not due to differential incidence of visual predation, nor, since they bear no relation to variation of habitat, to differences in its direction. In only two subareas do we think that visual selection is affecting morph frequencies.

The observed frequency distributions cannot be accounted for by sampling drift ('genetic drift') at the present day since the numbers involved are far too large and the frequencies too constant over large areas. In the few populations that have been observed for up to 10 years, no major changes of frequency have been found. The probability of a reduction to a few isolated populations because of ploughing up or drought in the last 200 years and subsequent drift and expansion is shown by the known agricultural history of the district to be slight. Restriction by spread of *C. hortensis* is also unlikely. A few colonies with restricted variation which might seem to show the action of drift or the founder effect are only extreme examples of local tendencies. Moreover, subfossil material from just off the south-western corner of the district strongly suggests that the area effects seen there have been in existence since Neolithic times.

A survey of another district of high downland (Lambourn Downs) has shown a similar state of affairs to that on the Marlborough Downs, with a large area characterized by excess of yellow and mid-banded, and adjacent to it localities in which visual selection is effective. Observations from various other places on and off the Chalk also indicate that area effects are frequent on the Chalk, but that away from it visual selection is the principal agent determining local variation in gene frequencies. There is good evidence that the pigmentation of the body, which is apparently multifactorially controlled, also shows area effects; and part of the correspondence between body colour and background shade reported by Cain & Sheppard may be due to them. The evidence available for *C. hortensis* suggests that this species also shows area effects in shell characters. Yellow, pink or brown may predominate in *C. nemoralis*, but area effects in banding seem due mostly to the excess or defect of the modifier M^3 which reduces the five-banded phenotype to the form with only the middle band.

It seems clear that the area effects are caused by some form of selection, but the topography, geology and vegetation of the Marlborough Downs gives no clue to what this could be for banding. Brown is known to be common only in the northern half of the range of *nemoralis*, and *hortensis* to extend much farther north than does *nemoralis*. A study of the distributions of the two species and of the brown morph on the Marlborough Downs suggests that local features of topography of open downland may produce localized climatic conditions influencing the relative distributions of the species and the abundance of brown. The abruptness of change of gene frequencies in both colour and banding might be caused by the change-over from one balanced gene complex to another requiring very different frequencies.

Examination of Fisher's equation for stability of a polymorphism maintained by heterosis (the most likely condition in these species) shows that in the districts where visual selection is effective in altering gene frequencies in *nemoralis*, the heterozygote advantage can only be of the order of a few percent, and that local differences of a few percent in the selective disadvantages of the homozygotes concerned could well produce area effects as marked as those we have observed.

For biological purposes it is essential to recognize the difference between changes in gene frequency caused by selection and those produced by the effects of sampling error. 'Genetic drift' has been generally used to refer to the latter, but Sewall Wright uses it for all apparently random changes, whatever their cause, and perhaps for all changes in gene frequency; we therefore use *sampling drift* for the effects of sampling error. Surveys based only on the observations of frequencies and population size in widely scattered populations do not allow one to distinguish between the effects of selection that varies in direction and intensity from place to place (although more or less

constant in time) and those of sampling drift. In general it is exceedingly difficult to identify the result of sampling drift in the wild except in certain situations. Casual collecting over such a district as the Marlborough Downs might well give the impression that sampling drift was effective there, but a more intensive survey shows the contrary.

I. INTRODUCTION

It is impossible to determine the relative importance of natural selection, genetic drift (sampling drift, see p. 59), and the founder effect in producing differences between populations in the wild, merely by inspecting the variation in proportions of given genotypes in different colonies and the differences in the size of the colonies. This may well be sufficient in the laboratory, if the environment can be considered identical for all populations; but this is probably never so in the wild, and can certainly never be safely assumed. Features of the environment that may affect gene frequencies must also be examined.

This paper presents a study from this point of view of populations of the highly polymorphic snail *Cepaea nemoralis* in an area of about 60 square kilometres on the Marlborough Downs, and supplementary studies elsewhere. It has been shown previously (Cain & Sheppard 1950, 1954, 1961) that visual selection by predators reduces the frequency of whichever phenotypes are conspicuous against a given background, and from this it was inferred that physiological selection, almost certainly favouring the heterozygotes, nevertheless maintains the polymorphism. In the Oxford district the result is that the colonies resemble their backgrounds well, but always contain a proportion of the more conspicuous forms. The present study shows that in a nearby area, physiological selection, probably in relation to local climatic differences, may play the greater part in determining gene frequencies, to such an extent that particular phenotypes may predominate greatly in particular areas (*area effects*, p. 14). A detailed study of gene frequencies and conditions in the Marlborough area also allows us to examine critically certain apparently anomalous colonies with greatly reduced genetic variation, which might appear to have been founded by very few individuals, or to exhibit the action of sampling drift.

II. METHODS

1. *Collections*

The great majority of the collections were made between March 1960 and July 1961. The colony at Sharpridge 2 was visited frequently from April 1959 to October 1961. Colonies at Rockley (1 to 9), Rough Down, Shoulder of Mutton 1 (= Hackpen Wood) were first visited by A.J.C. and Dr P. M. Sheppard in 1951 (Cain & Sheppard 1954; Sheppard 1952). Rockley 2 and 3 were first visited by Cain & Sheppard in 1950.

The present investigations were begun in order to sample colonies close to Sharpridge 2 which was discovered (by J.D.C.) in 1958 and recognized as having remarkably few genotypes; it was desired to know how close were the nearest occurrences of the genotypes that might be expected. It quickly became apparent that gene frequencies on the whole scarpland nearby were highly abnormal compared with previously recorded English colonies, and several collecting trips were made to find colonies over the whole district. Subsequently, special visits have been made to ensure a fairly uniform coverage, and to obtain as many samples as possible from the rarer habitats, such as mixed deciduous woods.

We have tried to visit all those types of habitat that exist in each part of the district, and to leave no major part at all suitable for *Cepaea* unvisited. Every kilometre-square in the district has been visited and several collections have been taken from most of them. In areas of particular interest, samples have been taken from several adjacent localities.

No attempt has been made to determine accurately the limits and density of the populations of *Cepaea*, except at Sharpridge, since this would require an investigation by capture–recapture methods or exhaustive search during favourable weather of all the habitats suitable for *Cepaea*. Rockley Down 3, for example, is very steep downland with turf and nettles. It was visited on a highly favourable day in spring (mild, humid and not very sunny) and 292 live snails were picked up by two collectors in about a quarter of an hour over an area not much more than 30 m square. Yet no predated shells and very few dead ones were seen. On an unfavourable day, when the live snails were buried, a collector might well conclude that the species was rare there, instead of extremely abundant.

At the localities shown in table 1 all the specimens seen during collecting trips, whether predated, dead intact, or live were collected, except at Sharpridge, where the snails were left *in situ* (and on one occasion at Preshute Down when a small sample was merely noted but not removed). In some other localities (figure 2) the occurrence of the species was noted but the snails (usually less than 5) were not collected. In no case, except at Sharpridge mentioned below, did the small samples depart from the general pattern of the distribution of phenotypes.

The visual selection exercised by certain predators is not great enough to produce serious bias when predated shells are used to obtain an estimate of the relative abundance of different phenotypes for the purpose of a general survey of an area (Cain & Sheppard 1950, 1954). A careful search was made at each locality where the snails were found, so that the sample obtained was as nearly random as possible. Cain & Sheppard (1950) pointed out that they themselves no doubt exercised a little visual selection in collecting, but that this could only decrease the observed association between shell-characters and habitat that they found. In the present investigation this slight departure from random sampling may result in a slight over-estimate of the more conspicuous shells, but any enhancement of the area effects (p. 14) is likely to be trivial, and visual selection can only be underestimated.

2. *Scoring*

The system of scoring bands and colours used by Cain & Sheppard (1950, 1954) has been used here. Previously mere traces of bands (i.e. tiny pigmented areas only just behind the lip) were not reported, since it was evident that these would be ignored by predators. In the present investigation, the occurrence in certain areas of any phenotype other than unbanded 00000 and mid-banded 00300 was of great interest. In consequence, as a precaution, we noted the occurrence even of traces of bands 1, 2 4 and 5 in shells, which, if these were ignored, would be classed as 00000 or 00300. Only a few were found. The genetics of traces is unknown.

No consistent nomenclature for the genes so far recognized as concerned in the polymorphism of *Cepaea nemoralis* has yet been produced. The notation given by Lamotte (1954) for some genes affecting banding does not seem to be in agreement with modern usage.

In this polymorphism it is difficult to consider any one of the colour or banding varieties as the wild type, since all have some claim to this title (although Cain, King & Sheppard (1960) in agreement with many previous writers have suggested that yellow five-banded may be the original form, on which the rest of the polymorphism has been superimposed). Also the polymorphism is certainly not yet fully explored genetically, and it may well be necessary in the future to interpolate newly recognized allelomorphs into the dominance hierarchies already worked out. Consequently, any system which involves a special nomenclature distinguishing wild types or recessives is hardly applicable here, and is liable to the grave defect of name-changing with increase of knowledge. In the following system we indicate the loci and distinguish the different allelomorphs by symbols unique at each locus, but do not show dominance relationships in the symbols. This nomenclature should require only additions as further allelomorphs and loci are distinguished, and alteration only if a locus becomes separable into two closely linked loci.

The genes considered in this paper are as follows, in dominance-hierarchy order for each locus beginning with the generally dominant form. Further data are given by Cain & Sheppard (1954, 1957) and Cain *et al.* (1960).

(1) *Ground colour of shell*

Brown G^B, dark pink G^{DP}, pale pink G^{PP}, dark yellow G^{DY}, pale yellow G^{PY}. Also in this series with dominance relations as yet unknown are: faint pink G^{FP}, and yellow white G^{WY}.

(2) *Banding*

Bands absent 00000 B^0, bands present B^B.

(3) *Suppression of certain bands*

Mid-banded 00300 M^3, unmodified M^-. Upper bands suppressed 00345 U^{345}, unmodified U^-.

(4) *Alleviator of band suppressor*

Spread bands S^S, unmodified S^-.

(5) *Pigmentation of lip and bands together*

Normal dark lip and bands P^B, unpigmented lip and bands (so-called albino including roseozonate and hyalozonate) P^T.

The loci G and B are very closely linked; S and P are probably linked to them, but M is independent, as is U (Lamotte 1954).

In the new variety spread bands, investigated genetically by Cain *et al.* (1960), there is a strong central band on the shell with, on either side, at least near the lip, indistinct smudges of pigment representing some or all of the other bands. Rarely, these may be so distinct as almost to appear like full bands, but their edges are never clear-cut and the middle band is far more emphatic. In heavy manifestations, there may be almost the appearance of a complete fusion of all five bands (12345), but on the higher parts of the shell, the middle band can be seen to predominate. In slight manifestations there is only a dingy tinge of pigment on either side of the middle band close to the lip. A spread-banded shell never presents the vigorously stripy appearance of normal five-banded shells. In previous papers by Cain & Sheppard, this form had not been recognized as genetically

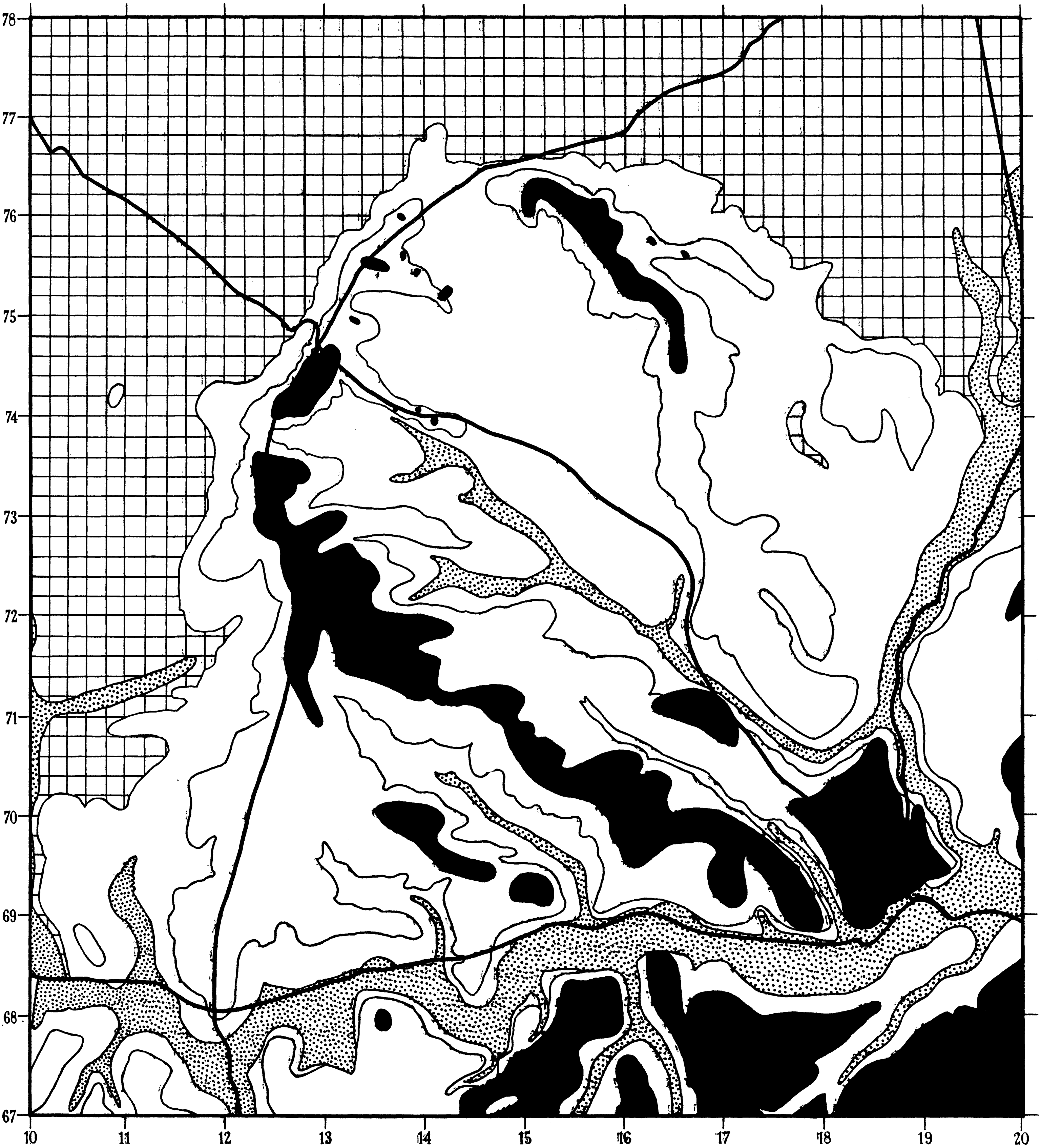

Figure 1. Geological map of the Marlborough Downs area (based upon drift 252, sheet 266 of the Geological Survey of England and Wales, 1925). Lower Chalk check-shaded; Middle and Upper Chalk white (boundary of Upper Chalk shown); clay-with-flints black; alluvium and valley gravel stippled. Some roads and the Ridgeway are shown in solid black lines. Kilometre lines of the National grid marked. All maps are orientated with the National grid north at the top. *Crown copyright reserved.*

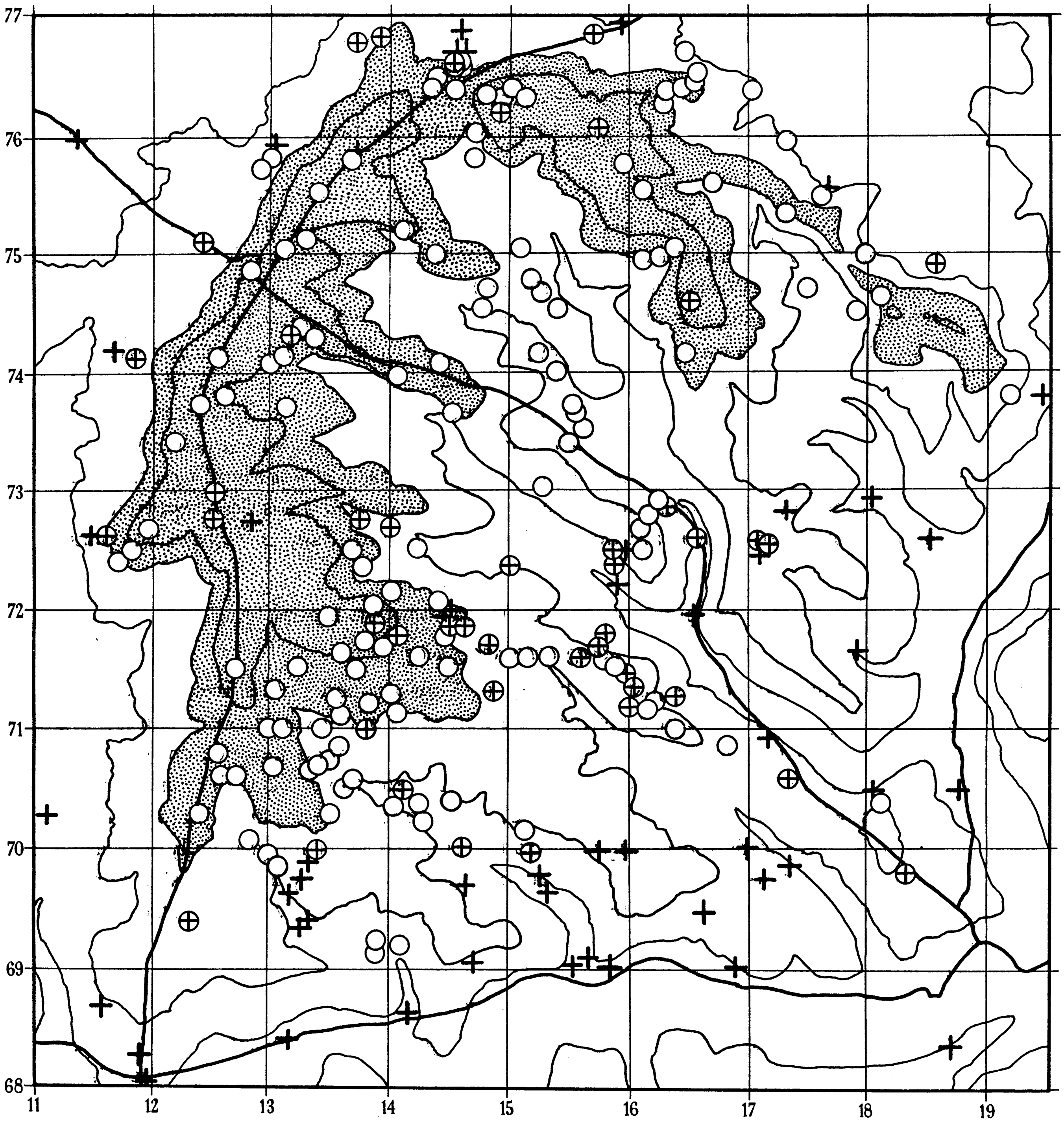

FIGURE 2. Map of all observed localities for *Cepaea nemoralis* and *C. hortensis* on the Marlborough Downs, in relation to altitude. Only *C. nemoralis* observed, circle; both species observed, circle with cross; *C. hortensis* only observed, cross. Contours at 100 ft. intervals, land over 700 ft. stippled. This map shows a few localities where only single shells or very small numbers were observed, which do not appear in later figures. Kilometre squares of the National grid shown.

distinct; the slight manifestations were grouped with the mid-banded form, 00300, and the heavier ones as variants, with more or less fusion of bands, of the five-banded 12345. In the present paper spread-banded shells are recorded as such (tables 1 to 4), but for comparison with Cain & Sheppard's results shells heavily pigmented above the mid-band have been scored as effectively banded, the rest as effectively unbanded. Genetically all forms of spread-bandeds have been considered as a modification of the mid-banded class, 00300.

Scoring of the body colour (§XI) has been done with the Villalobos colour atlas (1947) in the manner described by Cain & Sheppard (1952), except that matching was done under artificial (fluorescent) lighting instead of at a north-facing window. (One sample was scored under both conditions; the scores showed good agreement.) The distribution of pigment over the visible parts of a snail's body varies considerably from individual to individual. Some are almost uniformly grey; others have a rather dark forehead with two dark stripes extending back from it along the dorsum, and pale sides; in a few the sides may be much darker than the dorsum. Consequently we have also scored an area on the side of the body just behind and below the origin of the upper left-hand tentacle. Although both scores are necessary for any detailed work on body colour, it was found that there is a strong correlation between them. Consequently, only the forehead has been reported here, since the data obtained with it are directly comparable with those of Cain & Sheppard (1952).

III. Description of the Marlborough Downs

1. *Topography and geology*

The district investigated lies just north-west of Marlborough (Wiltshire) between the valleys of the Og and Kennet, and apart from small areas of alluvial deposits consists of a dissected plateau of Upper and Middle Chalk resting on a much more extensive one of Lower Chalk (figure 1). The highest points are at about 850 to 890 ft. at the northern and western edges, with a steep scarp face (figure 2) down to the Lower Chalk plain (which is at about 600 ft.). Running south-eastwards from the highest areas and gradually decreasing in height to about 550 to 600 ft. are long ridges of chalk separated by dry valleys, in some of which are alluvial deposits. In the valley running by Rockley village a stream, the Rockley Bourn, flows every few years in wet winters, and is then the only running water on the Downs.

2. *Vegetation*

Much of the area is now ploughed up but on the higher parts, along some of the steepest valley sides, and in some areas in the south-west with an abundance of sarsen stones (large sandstone boulders strewn over the surface) there is much downland grass. At the present day, some areas of grassland have been maintained as gallops for exercising racehorses, and *C. nemoralis* occurs on at least one of these. The general characteristics of chalk grasslands have been well summarized by Tansley (1939). They are widespread over the Chalk and maintained primarily by grazing (by sheep and rabbits). When grazing is prevented they are rapidly invaded by juniper (*Juniperus communis* L.) and hawthorn (*Crataegus monogyna* Jacq.), eventually becoming beechwoods (*Fagus sylvatica* L.). The elder (*Sambucus nigra* L.) is a common shrub or small tree especially associated with rabbit warrens

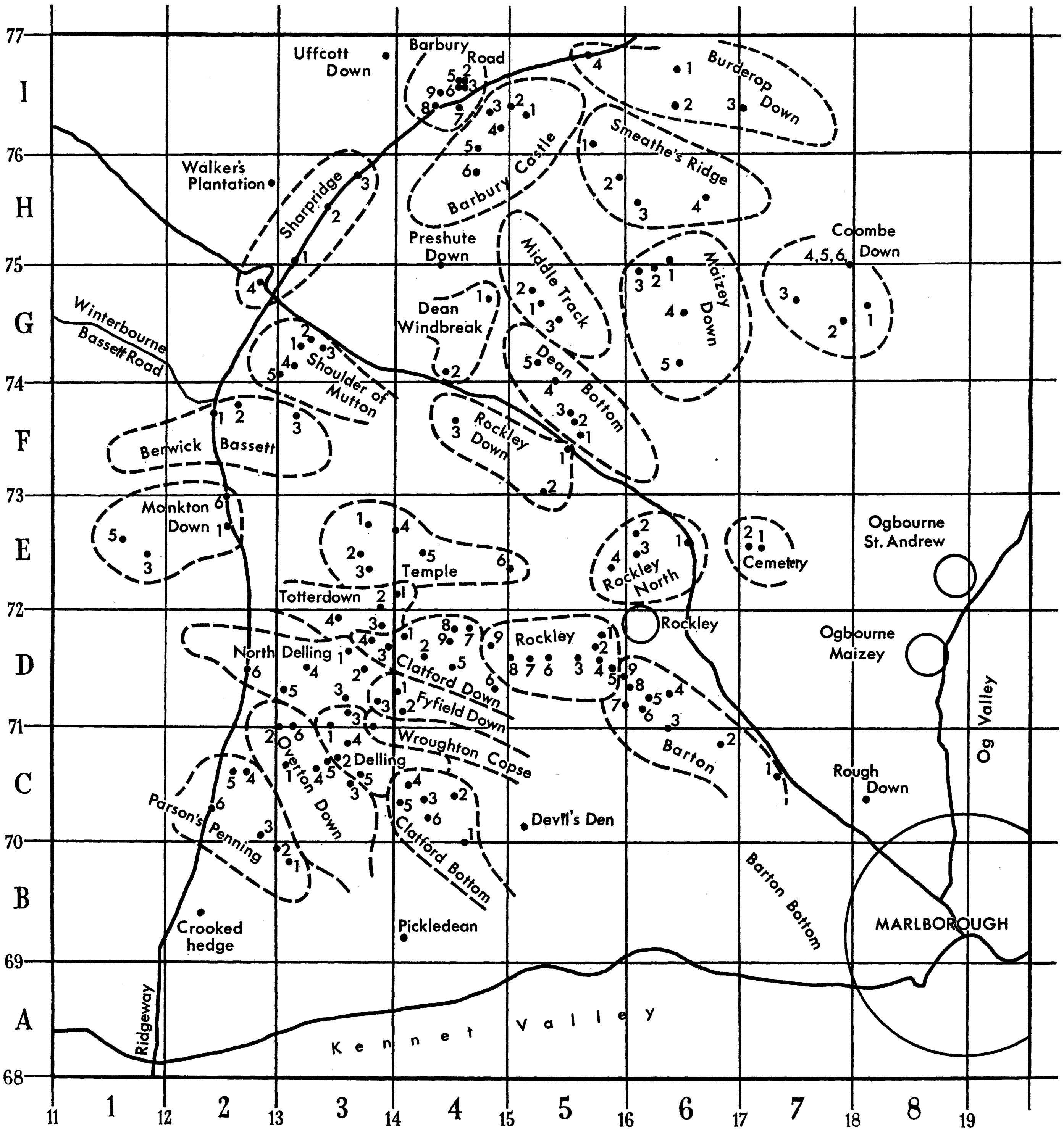

FIGURE 3. Geographical distribution of our localities on the Marlborough Downs, with names of localities and other features. Each square has a letter and figure which is quoted in the text after locality names to facilitate finding them (e.g. Crooked hedge, bottom left-hand corner, is in square 2B). Kilometre squares of the National grid shown.

Figure 4. Land available to *Cepaea* on the Marlborough Downs, 1960. Woods black, other habitats (downland, hedgerows, strips along fences, roads and other boundaries) stippled. The large circle encloses an urban area (town of Marlborough) with little space available to *Cepaea.* Areas in the Kennet and Og valleys, close to Marlborough, and on the Lower Chalk have not been surveyed in detail, and many more hedges and field boundaries exist there than are shown. A few more suitable strips may exist on the higher downs. Only compact areas of woodland are shown, but not scattered thorn scrub, even if locally dense.

since rabbits do not attack it. Juniper is rare or absent on the Marlborough Downs. Scattered over some of the higher downs and on undisturbed downland in the south-west are old hawthorn trees singly and in clumps, sometimes almost close enough together to be considered as thorn scrub. These areas are usually used as cattle pasture at the present day. Rabbits were formerly exceedingly abundant, especially in the south (Dr P. M. Sheppard, personal communication) but are now very rare, and most of the warrens are regressing from rough herbage (mainly nettles *Urtica dioica* L.) to grassland. A former high incidence of sheep grazing and attack by rabbits may well account for the scarcity of juniper (Tansley 1939, p. 375). Gorse (*Ulex europaeus* L.) occurs only very locally (e.g. near North Delling 6 (2D, see figure 3), Totterdown (3D), Maizey Down 5 (6G), Barbury Castle (5I) and on Smeathe's Ridge (6H) and apparently nearly always on clay with flints, presumably where leaching has rendered the soil somewhat acid, perhaps approaching chalk heath (Tansley 1939, p. 551). On Overton Down there are a few plants of heather, *Calluna vulgaris* (L.); the occurrence of this typically heathland species as scattered individuals on chalk has been discussed by Thomas (1960), who thinks it due to local acidity caused by ancient cultivation. Dr P. M. Sheppard informs us that there are a few plants also at Barton (6C).

There are no extensive woods, but in the south especially are a number of beech plantations and a few small mixed deciduous woods and copses (figure 4). We include with these a number of dense patches of elder and thorns, which are effectively woods for *Cepaea.* There are several beech wind-breaks lying athwart the valleys. A few conifer plantations exist, but *Cepaea* is not found in them. Of the woods, Wroughton Copse (mixed deciduous) is shown in Andrews and Dury's map of 1773. Early maps do not always show all woodland, and absence of a wood from a map may mean nothing. The Rockley North 1, 2 and 3 localities and Rockley 3 appear as woodland in the Tithe Award map of Ogbourne St

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DESCRIPTION OF PLATE 1

FIGURE 21. View from Clatford Down (Marlborough Downs) looking south-west to Overton Down, and including Wroughton Copse, Delling, and some Clatford Down, North Delling and Fyfield Down localities. Cultivation in foreground and extreme top left; remainder, ancient downland with scattered thorns and elders, two mixed deciduous copses (Wroughton Copse, upper left; the Delling, upper right) and one beech and conifer wood (upper right, obscured by shadow). Ridges are banks produced by ancient cultivation. Between the cultivated area in the foreground and the first track beyond it, yellows are at 80 % (Clatford Down 1) but at the isolated bush (strongly high-lighted) beside the further edge of the second track they are apparently absent and browns reach 93 % (Clatford Down 3). At Clatford Down 2 in (and to the left of) the bushes at the left-hand edge of the photograph between the two nearest tracks, browns are at 73 % and yellows at 13 %. The change-over from the area of excess yellows to that of excess browns takes place slightly beyond the nearest track and roughly parallel to it; and browns remain in excess to the upper edge of the photograph, except that in the bushes immediately left of the beechwood, yellows reach about 40 %. *C. nemoralis* is abundant on the grassland and occurs in the areas of woodland; *C. hortensis* is restricted to the bushes and trees at the edge of Wroughton Copse, where it is abundant. Approximate grid references of upper and lower reference marks, SU 129701 and SU 141718, respectively.

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Andrew Parish (1843) but not Rockley 1 and 2. The map in Smith (1885), drawn primarily to show earthworks and ancient monuments, has

(i) Wroughton Copse;

(ii) a plantation now vanished (Temple Down Plantation, also in the Tithe Award map for Preshute Parish, 1842/43, in the Wiltshire Record Office);

(iii) the three clumps at Sharpridge;

(iv) Shoulder of Mutton Plantation (with a northern piece now vanished—Shoulder of Mutton was reported in Cain & Sheppard's papers as Hackpen Wood);

(v) Four Mile Clump (Maizey Down 4, 6G);

(vi) Smeathe's Plantation (Coombe Down 3, 7G) much larger than now, and

(vii) Rockley Down Windbreak (Rockley Down 1 and 2, 5F). It does not show Delling Beeches (Overton Down 6, 3C), Old Totterdown, Barbury Hill Wood (Smeathe's Ridge 1, 5I), Nut Plantation (Burderop Down 1, 6I) or Dean Windbreak, but this last is marked in the Ordnance Survey map of 1901. Nor does it show the Avenue at Rockley (Rockley 1 and 2), which is shown in the 1843 Tithe Award map, but this was clearly omitted either by mistake or because it was associated with no important antiquities. The Ordnance Survey map of 1893 shows the three Sharpridge clumps and Shoulder of Mutton Plantation. It is probable that most of the woods, plantations and wind-breaks are more than 60 years old, and several are considerably older than this, notably Wroughton Copse which is known from 1773, but may be much more ancient, though not in existence in 1300 (Mr P. Fowler, personal communication).

Sheep and rabbit grazing have been important biotic factors on the Downs for centuries, and the grasslands on the higher downs have been comparatively stable, although large areas have been cultivated at certain periods. The valleys have probably been cultivated fairly continuously for a very long time.

3. *Habitats available to* Cepaea

Cepaea is not found on ploughed land nor on land heavily trampled by cattle. Consequently it is restricted to what is left of the open downs, to woods, to hedgerows and to grassy banks by fences. This allows for a wide distribution but at the present day many populations are isolated by cultivation. The areas occupied by old downland are shown in figure 4 together with field boundaries and roads, along which *Cepaea* can live in hedges or at the foot of fences. It has not been found in some apparently suitable localities, but intensive search under suitable weather conditions might well reveal it. The high downs are little visited, and contain no suburban areas; consequently human interference with the colonies (except for agriculture) is probably slight or absent.

IV. Distribution of Phenotypes on the Marlborough Downs

1. *Banding*

The localities of the samples obtained on the Marlborough Downs are shown in figure 3, and their compositions in table 1. It will be seen from this table that many have no or exceedingly few five-bandeds (including in this category all but unbandeds and mid-bandeds—i.e. including such forms as 00345 reckoned by Cain and Sheppard as effectively unbanded). These samples, moreover, are not distributed at random over the Downs but characterize the south-western half approximately (figure 5). In the area *A* in figure 5 bounded by Rough Down (8 C), Pickledean (4 B), Crooked Hedge (2 B), Monkton Down 5 (1 E), Walker's Plantation (2 H), Sharpridge 3 (3 H), Dean Windbreak (4 G), the Dean

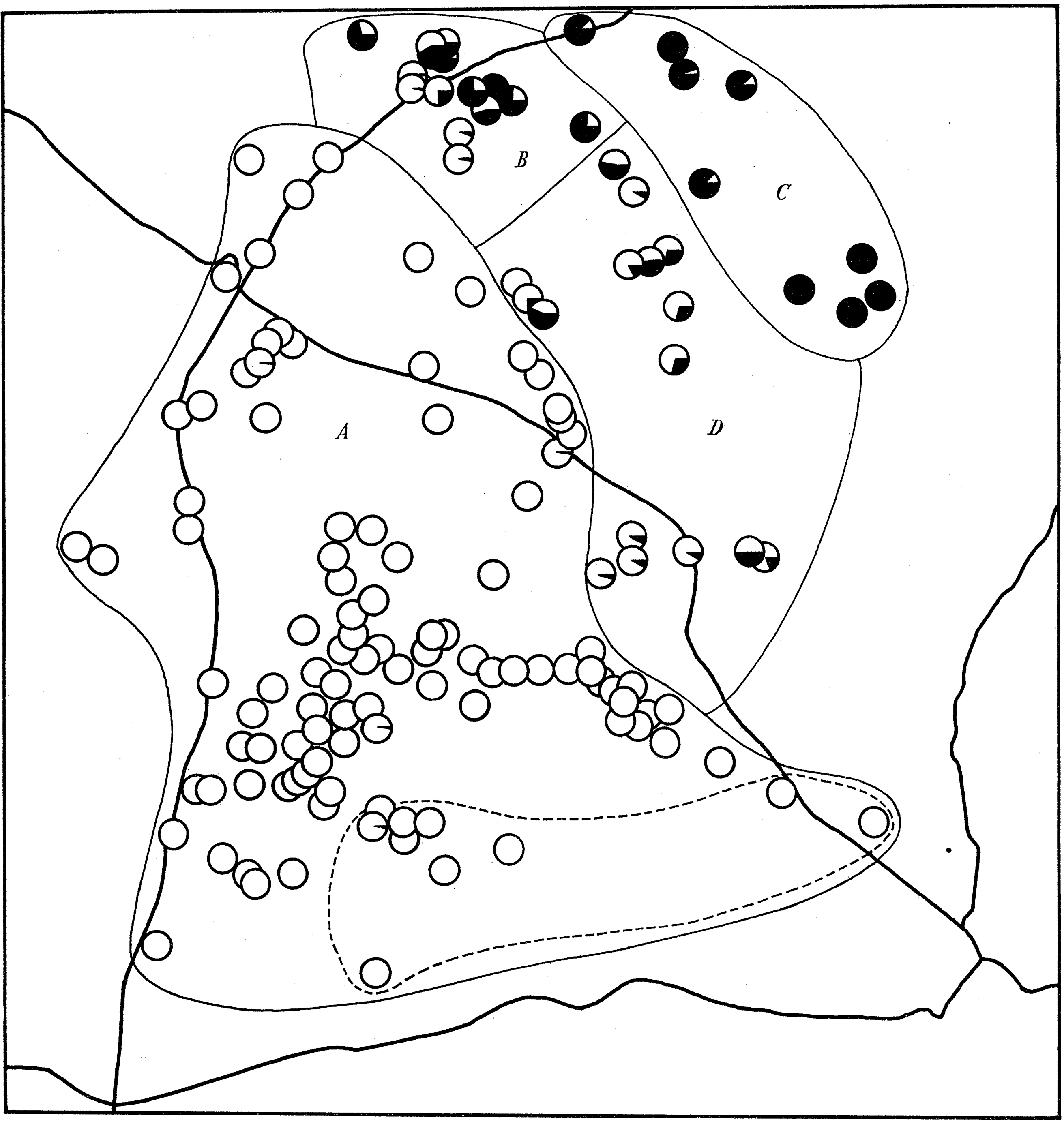

FIGURE 5. Proportions of five-banded shells and non-five-banded shells (00000 and 00300) in *C. nemoralis* on the Marlborough Downs. Proportions for five-bandeds in each sample black. *A*, non-five-banded area; *B*, Barbury area (transitional); *C*, five-banded area; *D*, southern intermediate area. The dotted line encloses colonies with a high proportion of spread-bandeds.

Bottom samples, Rockley 1 (5D) and Barton 4 (6D), only the following five-bandeds appear in our samples:

(4C) Clatford Bottom 5	1 (may be spread-banded)
(4D) Fyfield Down 2	1
(3G) Shoulder of Mutton 4	2
(5F) Rockley Down 1	1

Slight traces of bands other than the middle one have been seen in brown shells at Clatford Bottom 2 (one), Wroughton Copse (two) and Devil's Den (one) but their significance is doubtful.

In addition we have seen but not collected a single yellow five-banded between Sharpridge 1 and 2, and one juvenile brown five-banded at Devil's Den; in intensive searches at Rockley 1 to 9 (5D) Dr P. M. Sheppard found only three five-banded individuals amongst a very large number of unbandeds and mid-bandeds. This makes a total of only eleven five-bandeds in more than 5767 snails from 103 localities. The area is bounded on the west and south and along the valley from Rough Down (8C) to Barton 4 (6D) by colonies of *C. hortensis*. On the north and north-east are populations of *C. nemoralis*, which do have five-bandeds. At Barbury Road 7 and 8 (4I), Barbury Castle 6 (4H) and 5 (4I), and Rockley North 2, 3 and 4 (6E), all on the north and east borders of the non-five-banded area, the percentages of unbandeds and mid-bandeds are still 90% or more. In the Barbury area (area *B*, figure 5) from which we have several large samples, there is a most remarkable sudden decline from approximately 98 to 34% over only 450 m (from Barbury Road 8 (4I) to Barbury Castle 3 (4I)) and from 94 to 34% between Barbury Castle 5 and Barbury Castle 3 over only 320 m. The samples from the Burderop Down to Coombe Down area (area *C*, figure 5) continue this trend, having percentages of unbandeds and mid-bandeds below 20, and indeed, the samples from on or near Coombe Down have almost nothing but five-bandeds. The area (*D*, figure 5) geographically intermediate between that just described (*C*, figure 5) and the non-five-banded area, is unfortunately not very rich in *Cepaea*, as a great deal of it is under cultivation. What samples are available indicate a transition from north-east to south-west from low to high percentages of unbandeds and mid-bandeds, as might be expected; and in at least one place (Smeathe's Ridge 4 (6H) to Smeathe's Ridge 3 (6H)) it seems as steep as at Barbury Castle (13 to 91% over 550 m.)

An absence of the five-banded phenotype is most unusual in *C. nemoralis* in Britain; of the 102 samples of more than 20 shells reported by Cain & Sheppard (1954) from localities outside the Marlborough Downs, only one has no five-bandeds. Further collection by us (table 4) has produced out of eighteen populations from localities not on the Chalk none which have no five-bandeds, and only three (Knoll Down, Knoll Down Roadside and Dogtail Down) out of 49 on the Chalk.

If anything could be more surprising than the existence of so large an area on the Marlborough Downs with virtually no five-bandeds, it is the sharp juxtaposition to it of an area very heavily five-banded. It will be shown later (p. 21 below) that this cannot be due to variation caused by visual selection in relation to background.

It is known that M^3, producing 00300, is a modifier of B^B which produces 12345, at a locus not linked to it or to colour, and that B^0, responsible for 00000, is a dominant allelomorph of B^B, the locus for which is very closely linked to that for shell colour. Consequently the virtual absence of the 12345 phenotype but the occurrence of large numbers of 00300 in the virtually non-five-banded area means that B^B, the gene for 12345, is common and widespread in this area, but the populations are saturated with the modifier M^3, and consequently, although there is no linkage between the loci B and M, B^B is hardly ever expressed phenotypically. Other modifications of the 12345 phenotype, such as 00345 which occurs in the north-eastern area, may be common in the non-banded area, but as they will be suppressed by B^0 and M^3, nothing can be said about them in that area without extensive breeding experiments.

Well-marked banding is rare in browns (Cain & Sheppard 1954; Cain *et al.* 1960), in which colour it is absent over the greater part of the Marlborough Downs area except for one or two scattered single examples. But at Barbury Castle 3 (4I), there is a surprising abundance of five-banded browns (18 out of a total of 21 browns).

The phenotype spread bands is rare over most of the Marlborough Downs (as it is elsewhere except on the Lambourn Downs), but in the extreme south at Barton 1 (7C), Rough Down (8C), Clatford Bottom 1, 2, 3 and 5 (4C), Devil's Den (5C) and Pickledean (4B) it is relatively common (more than 30% of the mid-banded shells, usually over 50%). These localities are all at extreme positions to the south and south-east in the range of *C. nemoralis*. There is an additional minor centre of abundance at Monkton Down (1E). In the south and south-east the strip containing localities with many spread-bandeds cuts across the areas defined by abundance of particular colours, since at Pickledean pinks are most abundant, at Clatford Bottom browns, and at Barton Down yellows.

Such phenomena as these just described, in which, throughout an area large compared with the area occupied by a panmictic population of *Cepaea*, one colour or banding variety is predominant, or at an unusually high frequency throughout without regard to habitat, we refer to as *area effects*.

2. *Colour*

Area effects are shown on the Marlborough Downs almost as well in shell-colour as in banding (figure 6). Brown, which is dominant to other colours, is very uncommon over much of the Downs, with a small centre of relative abundance (up to 28%) in the Barbury area (4I). But in most of the southern third and in a small area north-east of it comprising Rockley Down 1 and 2 (5F) and Dean Bottom 1, 2 and 3 (5F), brown occurs in remarkable abundance, reaching on open downland 68% in Dean Bottom and 93 to 98% in the Overton Down-Delling-Totterdown areas.

Outside the area of excess browns, in which pinks and yellows are necessarily few, pink (recessive to brown, dominant to yellow) reaches high proportions only in some places along the high downs and the scarp face, from Crooked Hedge (2B) round in a horse-shoe to Smeathe's Ridge 4 (6H) and again at Pickledean. Except at these few places, yellow is almost always over 60% in the northern half of the district, and in an area including Sharpridge 1 (3H), Middle Track (5G), Dean Bottom 5 (5G), Preshute Down (4H), Dean Windbreak (4G) and Rockley Down 3 (4F), one including Monkton Down 3 and 5 (1E) and Berwick Bassett 1 (2F), and again at Coombe Down 1, 2, 4, 5 and 6, it is over

80%, reaching 100% at Dean Windbreak 2 (4G). Since most of the habitats visited in these areas would be expected to have many yellows, a study of variation in relation to habitat is necessary to see whether area effects can be claimed.

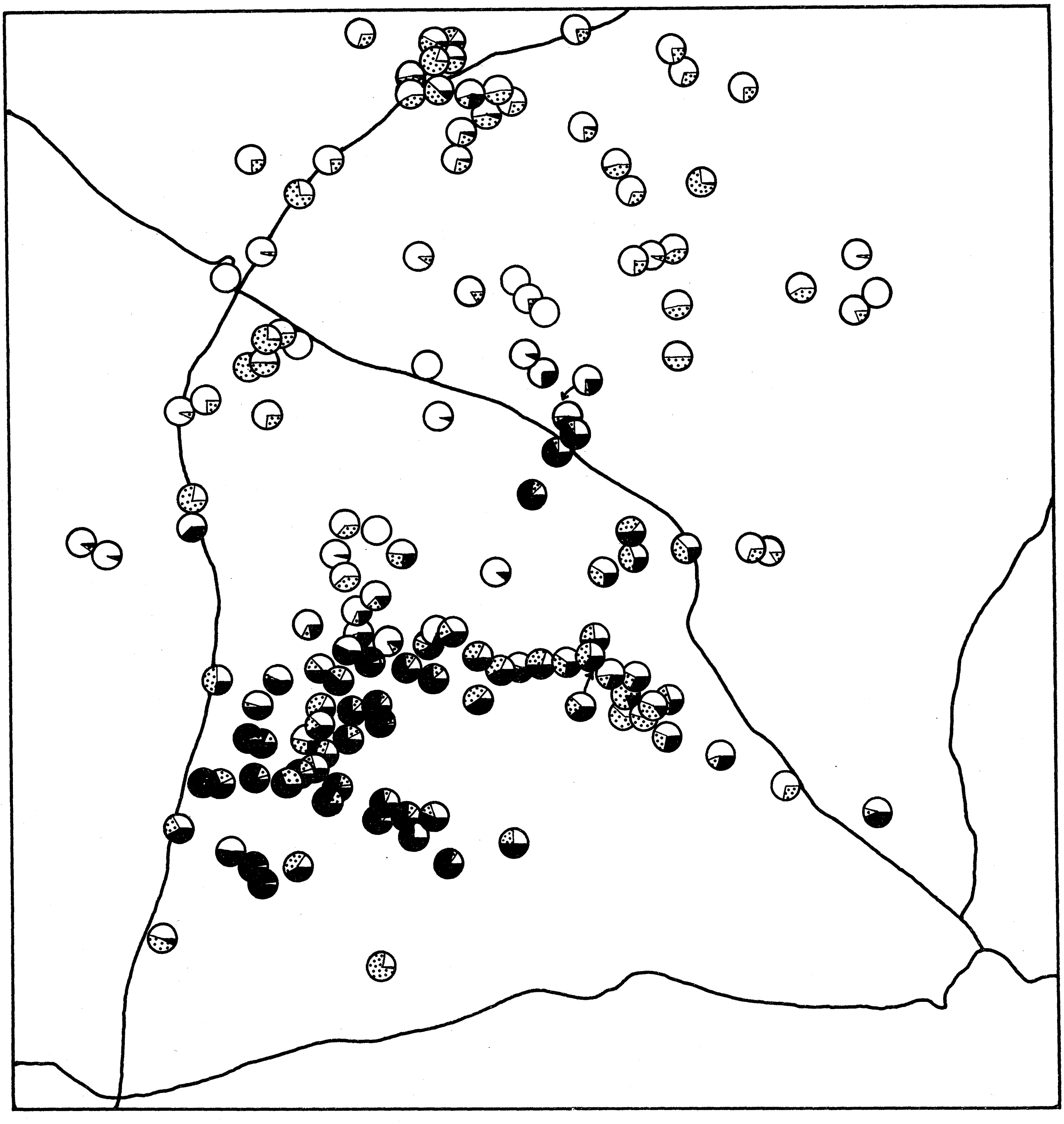

FIGURE 6. Proportions of yellow, pink and brown shells in *C. nemoralis* on the Marlborough Downs. Browns, black; pinks, stippled; yellows, white.

The most remarkable change in proportions of colours and the steepest phenotype cline we have found occurs on part of the northern edge of the excess brown area, where over a distance of approximately 130 m (and perhaps less than this) between Clatford Down 1 and 2 (4D) the frequency of browns changes from 12 to 73 %, and that of yellows from 80 to 13 %. (Pinks go from 8 to 13 %.) The change between Clatford Down 1 and 3 (4D and 3D) over about 150 m, is to 93 % browns and 0 % yellows with pinks remaining at about 7 %. Moreover, in going from Clatford Down 1 to 2 and to 3 we have seen live snails scattered in the intermediate area, and there is no reason to believe that the populations sampled at these three localities are in any way isolated from one another, except by distance.

To the south of this remarkably abrupt cline there are consistently high frequencies of brown for some distance, in fact nearly to the southern edge of the *C. nemoralis* populations. To east and west of it are less abrupt clines tending in the same direction. To the north, except at Temple 5 (4E), (formerly a small wood according to an Ordnance Survey aerial photograph taken in 1947) the frequency of browns remains low, becoming very low indeed in the Berwick Bassett 3 (3F), Rockley Down 3 (4F) and Dean Windbreak area (4G), and the frequency of yellow is high to very high.

The environment in the very small area containing Clatford Down 1, 2 and 3 gives us no clue to any selective force that might produce this extraordinary cline (figure 21, plate 1). There is a gentle and nearly uniform slope of downland with a gradient of about 1 in 16 declining nearly north and descending to a very shallow valley bottom with a gradient of only 1 in 18, with Clatford Down 1 on the bottom and 2 and 3 about 5 to 10 m in height up the slope to the south. The valley bottom has many scattered sarsens and much downland grass, and a few clumps of thorn and elder. The slope hardly differs from it except that there are no sarsens and the grass is rather less luxuriant. Thorns and elders are scattered in almost exactly the same manner over it. Clatford Down 3 lies on clay-with-flints while 1 and 2 are on chalk soils; but there is no correlation between the type of soil and the distribution of colour frequencies generally over the district (figures 1 and 6). Neither aspect, topography, soil nor vegetation, therefore, give any clue to the reason for the existence of this cline. A single *C. hortensis* was seen at Clatford Down 1, but none at nearby localities except Totterdown 3 (3D).

3. *Variation with habitat*

(*a*) *Backgrounds*

To demonstrate variation with habitat, Cain & Sheppard (1950, 1954) visited, with very few exceptions, only areas with large stretches of easily definable habitats. Nearly all classes of habitats that they recognized differed considerably and consistently in either colour or the degree of discontinuity of the background at ground level; dense beechwoods, for example, having much red-brown leaf-litter covering large areas continuously, and blackish soil and dead cupules; mixed deciduous woods having much pale brown leaf-litter and some herbage and brambles giving a more variegated background; short turf being almost wholly green. They were able to use their simple classification by type of vegetation as a classification by general colour and stripiness of background. However, some habitats such as hedgerows were more varied than others of stricter definition, such as dense beechwoods; and they encountered two examples (Pan's Hill and Great Copse, Chislehampton) in which the background was highly exceptional for the class of habitat but nevertheless the colonies fitted the background.

For comparison with the present findings, figure 7 gives a scatter diagram of percentage yellows against percentage effectively unbanded shells based, with a few additions, on their collections from the Oxford district, but omitting all samples from the Chalk, which it will be shown require separate treatment. Figure 8 shows a number of additional collections made by us, also from districts not on the Chalk, and these tend to confirm Cain & Sheppard's results. The new data are given in table 4.

In the present investigation, we have had to look for colonies on the Downs almost irrespective of their background. Moreover, on the Marlborough Downs, some types of vegetation occur only sparsely, and then are intermixed with other types. Some woodlands, e.g. Smeathe's Ridge 1 (5I) and Dean Windbreak 2 (4G), are very open with an almost continuous grass cover; consequently, if visual selection is important there, one would expect in them a high proportion of yellows, as at Great Copse, Chislehampton (Cain & Sheppard 1954). In several cases the collection, of predated shells, was made under an isolated thorn tree, or in a minute chalkpit, perhaps 5 m square, containing a few bushes or brambles, or in scattered clumps of nettle, all surrounded by open downland. Without very careful investigation, one cannot determine exactly what proportion of the snails was living in the collecting area and what on the surrounding grassland, but from the relative extents of the types of habitat, one can usually be reasonably sure of what background the majority of the local population live on. Consequently the simple scoring used by Cain & Sheppard is hardly appropriate for this study, except for such types as dense beechwood or pure open downland grass, in which the colour of the habitat hardly varies. Indeed, it may even be seriously misleading, as when a collection under an isolated minute clump of thorn and elder bushes must be classed as in mixed deciduous woodland, but all the snails live on surrounding grassland and are brought under the bushes by thrushes for breaking.

We therefore use the following classification of habitats: dense beechwoods, dense oakwoods, dense mixed deciduous woods, open woodland (with a mainly green background at ground level), hedgerows, rough herbage (i.e. nettles, thistles, dock, burdock and other broad-leaved herbs, but not, or not much, grass), grassland (long grass, mostly on open downland), nettles in grass, and short turf. Where the actual place of collection is under scattered bushes or among very small nettle clumps in downland, the habitat is given as grassland. In a few localities, we have been reduced to describing the vegetation as mixed; in most of these there is a mixture of trees, shrubs and grass or rough herbage. Since the nature of the habitats in this area is of particular importance, and moreover since some may change with time, detailed descriptions are given in appendix 1, in which both the habitat at the collecting place and that surrounding it (if different) are given. It happens that oakwoods are not found in the Marlborough Downs district. Only three localities have much gorse; although it may be the major component of the habitat, it appears to be nearly as repellent to snails as are conifers. The ground beneath gorse is often very dry, and is usually covered with an apparently distasteful layer of sheddings. The specimens found beneath gorse bushes are almost always predated ones, presumably brought in from the grass nearby; gorses therefore have been included with grassland.

(*b*) *Incidence of predation*

It can be seen from figures 9 to 11 that the areas delimited by considering the composition of samples of *C. nemoralis* are not also each characterized by a predominance of one sort of background. Moreover, at least in the non-five-banded area (figure 9) woodlands do tend to have less yellows than do other habitats. But some of them, at least, have few yellows because that is a characteristic of their area. The area effects cannot therefore be explained by visual selection. Within each area there is some diversity of habitat (unfortunately very little in the north-east) which would be expected to provide the opportunity for visual

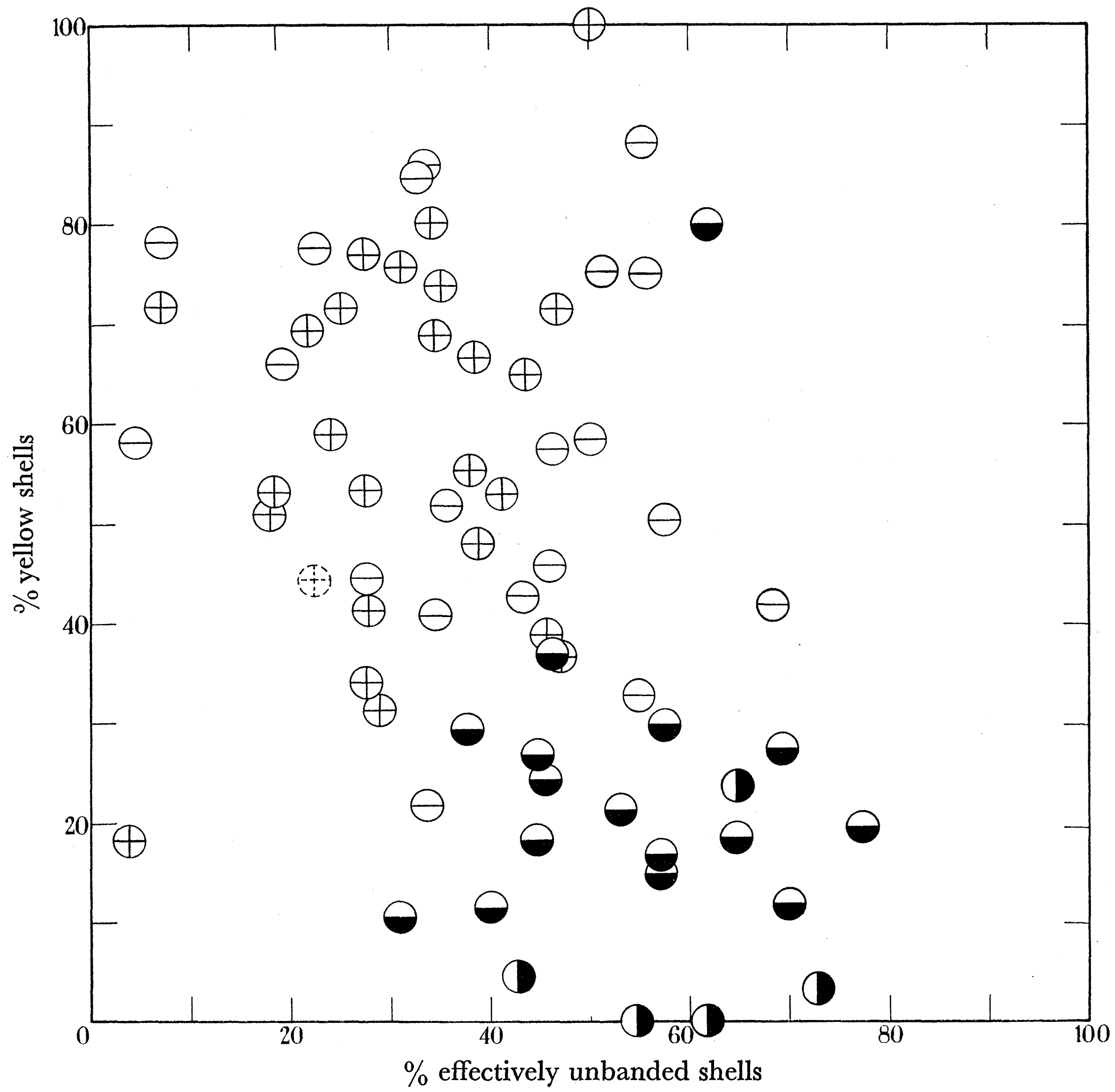

FIGURE 7. Scatter diagram for percentage yellow shells, percentage effectively unbanded shells, and habitat, of samples of *C. nemoralis* from localities within 10 miles (16 km) of Oxford. Based on Cain & Sheppard (1954) with some additions.

Key to habitat symbols

Small samples (less than 21), broken lines

Woods

● beechwoods
◑ oakwoods
◒ mixed deciduous woods
◍ open woods

Other habitats

⊕ hedgerows
⊖ rough herbage
⦶ nettles-in-grass
⦷ long grass
○ short turf
⊘ mixed

selection and a resulting resemblance of colonies to backgrounds, unless, of course, visual predators are unimportant or absent.

The song-thrush is certainly uncommon on open downland, and seems to prefer the close neighbourhood of trees or thick shrubs, perhaps not usually feeding more than 250 m from them, and then usually choosing an anvil well in the protection of a bush, rather than a stone out in the open. In our collections of predated shells, some may have been broken by small rodents (and perhaps rabbits) which break in the main whorl of the shell. Thrushes on the contrary tend to break the apex by hammering the shell on their chosen anvil (Morris 1954). Some predated shells are either too broken, or broken to such a shape that one cannot be certain of which sort of predator took them. We have found undoubtedly thrush-broken shells in all our samples of predated shells, and have ascribed only a few to rodent predation. Large quantities of thrush-predated shells have been seen in the Rockley beechwoods (Rockley 1 to 3), Barton 8 and 9, Rockley North 1 to 4,

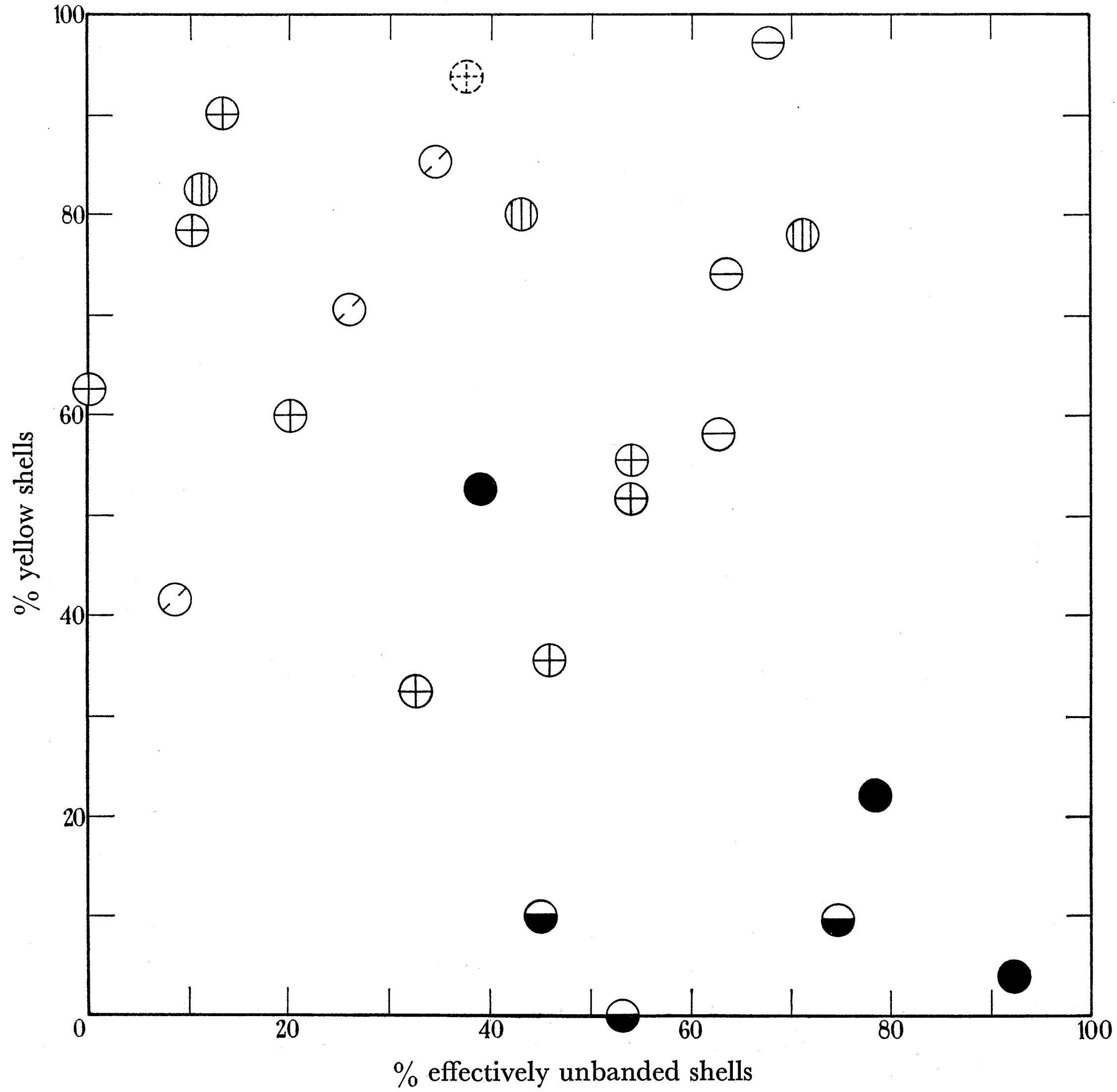

FIGURE 8. Scatter diagram (as in figure 7) for samples of *C. nemoralis* from localities outside the Oxford district and not on chalk, newly reported.

Clatford Bottom 1, 3 and 4, Overton Down 6, Wroughton Copse, Fyfield Down 2, Monkton Down 5, Clatford Down 9, Berwick Bassett 1, Dean Windbreak 2, Maizey Down 4, and Coombe Down 4; and thrushes are important predators elsewhere near trees and bushes. No predated shells of any sort have been seen at the Sharpridge colonies, and predation in general seems weak at the Dean Bottom and Middle Track colonies, the Barbury area, and indeed much of the open downland of the north and west. At Dean Bottom 2, where stones are rare, one was seen in a position sheltered by a small bush and ideal as an anvil but with no broken shells whatever around it, although snails were common nearby. What other species of bird may act as visual predators, but swallow the young snails whole and leave no shells as evidence of the predation is not known, and the absence of predated shells cannot be taken to mean the absence of visual predators.

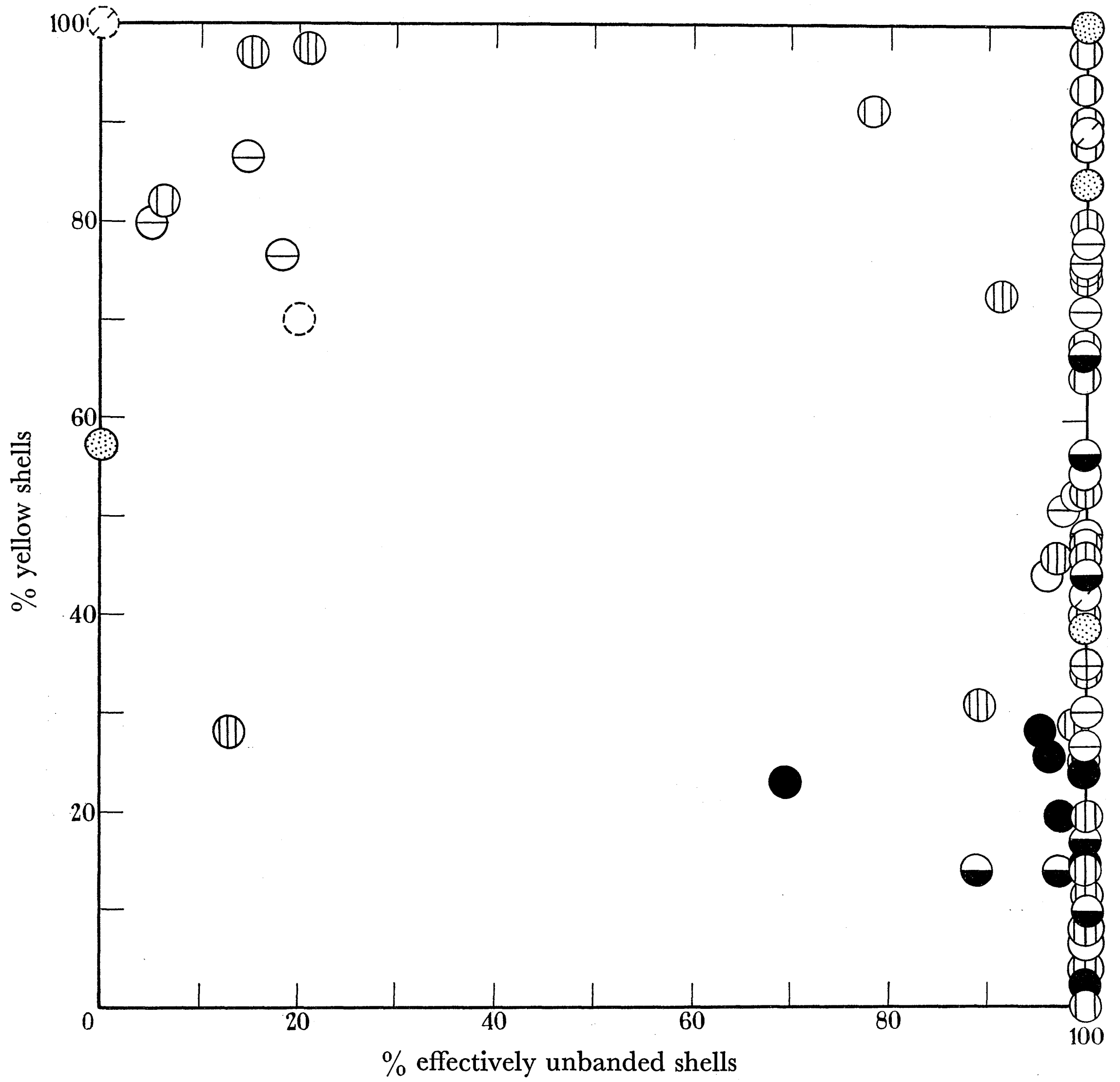

FIGURE 9. Scatter diagram (as in figure 7) for samples of *C. nemoralis* from areas *A* (right-hand side) and *C* (left-hand side) on the Marlborough Downs (figure 5). Only about half the localities at 100 % effectively unbanded are shown, for lack of space. Effectively bandeds in area *A* are nearly all heavy spread-bandeds, not five-bandeds. Effectively unbandeds in area *C* are mostly 00345, not 00300 and 00000.

Rodents, which are often important predators, probably predate not by colour but by tone (Cain 1953), and it is possible that in some localities they might produce a high proportion of pinks on open downland, since browns and yellows are not good matches for green grass. While a patchy incidence of rabbit predation might account for some local abundance of pinks on the Marlborough Downs, it cannot account for the area effects producing excesses of browns or yellows.

(*c*) *Banding* (figures 9 to 11)

The non-five-banded area *A* has a wide range of habitats including all those recognized in this paper except oakwoods; and by analogy with the Oxford district (figure 7) one would expect it to contain a correspondingly wide range of banding frequencies, but this is not the case (figure 9). Cain and Sheppard (1950), impressed by the general continuity of the short turf at Rough Down, considered that on this type of background, unbandeds and mid-bandeds might well predominate, and commented (1954) on the abundance of five-bandeds at Crowell Hill as unexpected. However, if one puts out a number of varieties on short turf, one finds that yellow five-bandeds appear to be better concealed than any of the unbandeds, although yellow unbandeds which have a dark body and appear green are quite easily overlooked. The reason for this is that although from a little distance, short green grass appears remarkably uniform, the narrowness of the blades does produce a considerable degree of discontinuity which is of the same order as that produced by the bands of the shell, and quite absent from beech leaf litter in which the component leaves are much larger than a single shell, and, moreover, tend to lie flatly on one another or on the bare earth. The correct explanation of the lack of banding at Rough Down can now be seen to be an area effect. This change of interpretation of the situation at Rough Down does not affect the general conclusions in Cain & Sheppard (1950) and (1954). The colonies on short turf should be mainly yellow and heavily banded. In long grass, which provides more cover, and in which there is much more opportunity for a snail to be seen with grass blades crossing it, a higher proportion of unbandeds might perhaps be expected.

In dense woods, as Cain & Sheppard (1950) pointed out, one would expect a large proportion of effectively unbanded shells, and this is indeed the case in the Oxford district and elsewhere (figures 7 and 8), but an absence of five-bandeds in large samples is found only on the Marlborough (and Lambourn) Downs, where it is clearly associated with an area effect.

In the heavily five-banded area *C*, there is no great diversity of habitats (figure 9), and the presence of much banding is what might be expected. Consequently we cannot distinguish here between area effects and visual selection. But the fact that so many of the effectively unbanded shells in this area are 00345, while 00000 and 00300 are very uncommon or locally absent (table 1 and figure 17*a*) suggests that an area effect is acting in the opposite direction to that influencing the non-five-banded area. This suggestion is strengthened by the situation in the Barbury area (figure 10), where again there is no great diversity of habitat but there is a considerable variation in the percentage of effectively unbandeds very strongly associated with geographical position, and forming a smooth transition (excepting only Uffcott Down) between areas *A* and *C*. Further south (figure 11) our rather scattered samples do show some correlation between banding and habitat, but this depends mainly on three Rockley North woodlands which, being adjacent to area *A*, may have too few five-bandeds. In fact, all the samples, when compared with those of the Oxford district, for example, are high in effectively unbandeds (00000 and 00300) and are probably affected by proximity to area *A*.

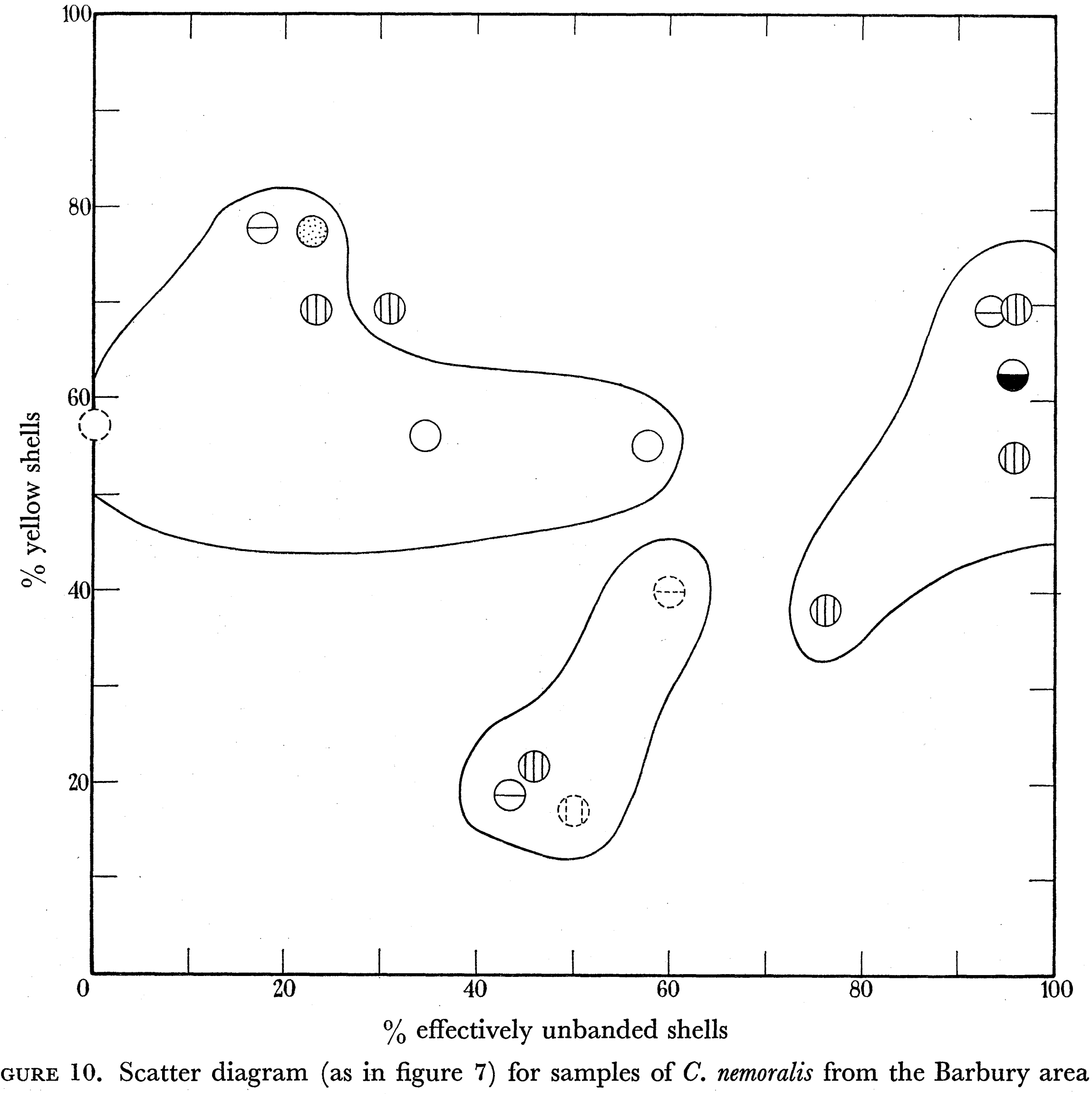

FIGURE 10. Scatter diagram (as in figure 7) for samples of *C. nemoralis* from the Barbury area (*B*, figure 5). Lines enclose localities geographically close to one another. Upper left, colonies near the five-banded area *C*; upper right, colonies near the non-five-banded area *A*; lower centre, colonies alongside the road running north through the middle of the Barbury area.

In short, then, over the whole of the Marlborough district there is no good evidence of variation in banding being associated with habitat. In some localities the banding is what might be expected from the background, but one cannot assert that this is produced by visual selection, and the strong association with geographical position seen in the samples from localities between the main areas would indicate that the occurrence of appropriate banding is the fortuitous result of area effects.

(*d*) *Colour*

There are two subareas in which thrushes are known to be predating and in which there is a good diversity of backgrounds from beechwoods to open downland, namely, at Rockley and around Wroughton Copse. The first of these has been described by Sheppard (1952) (Rockley 1 to 9); in it the proportion of yellows is higher on downland grass than in the adjacent beechwoods, the populations in which resemble each other in their high proportion of pinks (many of them dark pinks) and browns, as would be expected with visual predation. The two beechwood samples from Rockley North now reported agree well with those from the Rockley beechwoods, and that from Rockley North 4 (a grass sample) resembles Rockley 4. The sample from Clatford Down 6, which is only 300 m south of the Rockley colonies, is from a small patch of very dense thorns, with a dark brown background beneath them, and is not inappropriate to this background. Clatford Down 5, however, which is 400 m west of Rockley 9, is from open downland and its sample is completely

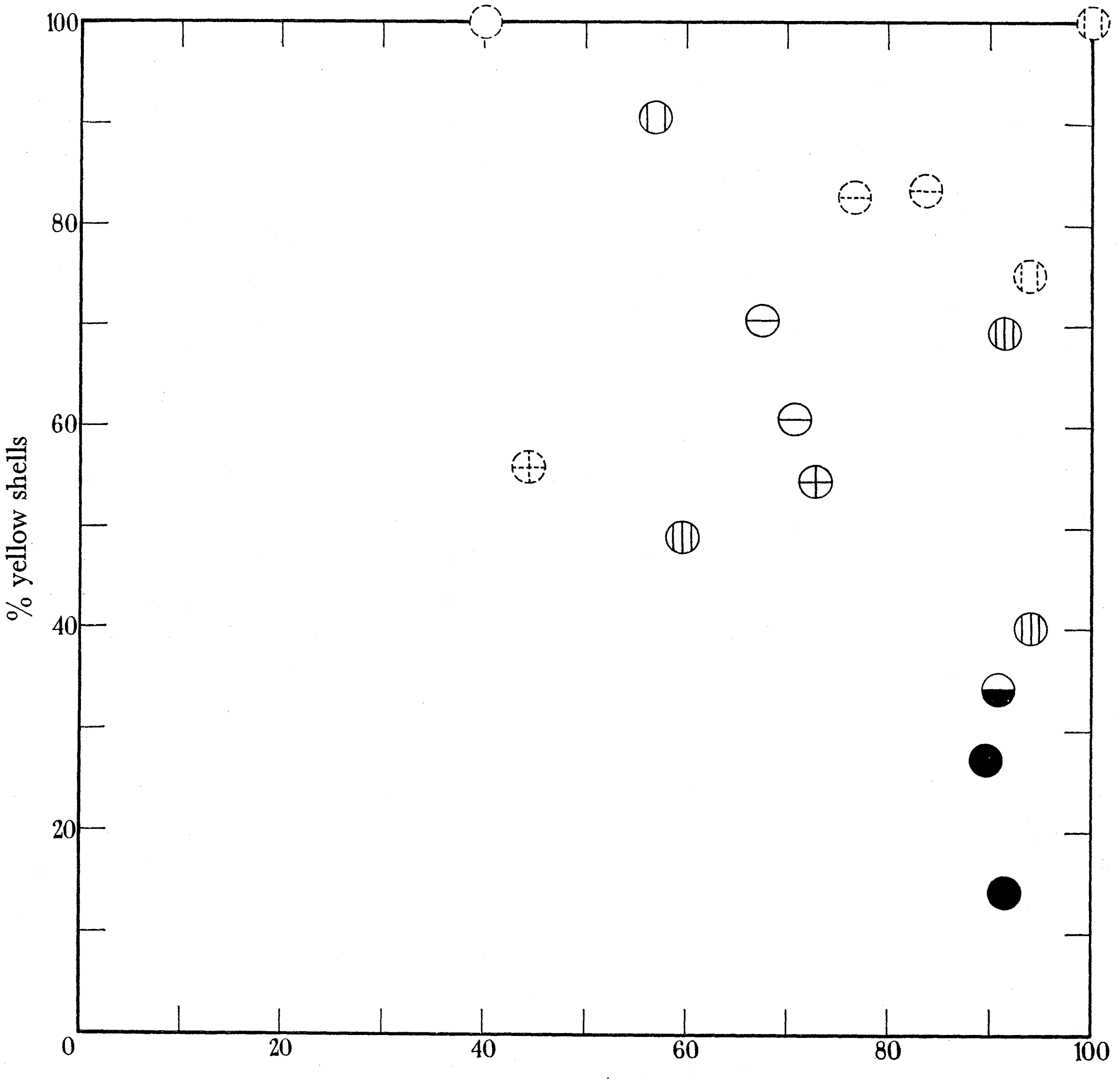

FIGURE 11. Scatter diagram (as in figure 7) for samples of *C. nemoralis* from the southern intermediate area (*D*, figure 5).

inappropriate; in fact it belongs by composition to the area with a great excess of browns, and is at the edge of it geographically. The downland sample Rockley 7 was taken from the grass east of Rockley 9, and around 8 and 6, and resembles those from 4 and 5, also downland. It is not known, therefore, where the area of excess browns ends and it may even include Rockley 9. It is true that this has a considerable proportion of pinks, but it is safer not to use it as evidence for visual predation. Clatford Down 6 has many pinks, and does not seem to belong to the excessively brown area.

The correspondence between sample-composition and colour of habitat in the Rockley samples, Rockley North 2 to 4 and Clatford Down being what would be expected from visual selection, and thrushes being known to predate extensively in most of these localities, there seems to be no good reason to doubt that visual selection on colour is effective there. However, the downland samples contain a considerable proportion of pinks and browns, although markedly fewer pinks (and rather fewer browns) than in the beechwood samples. If visual selection on open grassland is for yellows, one might well expect only a very few pinks and browns, not proportions of about 30%. It may be, then, that there is an area effect at Rockley producing a general small excess of browns even on open downland.

The second subarea includes Fyfield Down 2, Wroughton Copse, and Clatford Bottom 1, 3, 4 and 5, at which thrush predation does occur; it is characterized by an excess of browns, found also in the colonies nearby, except that browns are not more than 25% at Delling 1. Our first collections from here were at Overton Down 6, Delling 1 and Wroughton Copse, and from these alone there seemed to be as good a correlation between background and percentage of yellow as at Rockley, but the discovery of excess browns at Overton Down 2, Fyfield Down 2 and Clatford Down 5 made it clear that there was a strong area effect producing an excess of browns, and the low proportions of yellows in the beechwood and mixed deciduous wood (Wroughton Copse) were typical of the area, and need not be of their habitats. Exactly the same happened when Dean Bottom 1 and 2 were added to Dean Bottom 3 and Rockley Down 1. These examples show that no apparent correlation of sample composition and background in only two or three localities close together can be accepted as a demonstration of variation due to visual selection until the area containing them has been examined. One must have either a detailed examination of a given area, or many samples from each class of habitat over a large expanse of country before drawing conclusions.

That visual predation in the area of excess browns is being exerted in the expected direction is suggested by our collection from Fyfield Down 2 which contains both whole shells (mainly collected from the sides of sarsen stones where shaded by grass) and many thrush-predated shells from a group of stones under a bush. (Some rodent-predated shells may also be included but these should only decrease the effect observed, unless tone-predation is occurring which should be in the same direction here as predation by colour.) The broken shells consist of 125 browns and 0 yellows, the unbroken ones of 99 browns and 5 yellows, and the difference by exact probability test has $P = 0{\cdot}0183$. As some of the whole shells were dead and empty, it might be thought better to exclude them, and to regard only the live snails and the broken shells. This gives 75 browns and 3 yellows among the live snails, 125 browns and 0 yellows (as before) among the broken shells, and $P = 0{\cdot}0554$. Both probabilities suggest, and the former suggests strongly, that yellow shells are at an advantage to brown when visual selection is exerted. Wroughton Copse at least has been in existence (and most probably with thrushes in it) for a very long time, probably since the Middle Ages, and thrush predation is surely not merely recent in this locality. The extreme preponderance of browns, therefore, suggests a very strong non-visual selection, able to override the effects of visual selection almost wholly.

Outside these two subareas, probably the only locality where visual selection can be reasonably asserted from a correspondence between sample composition and habitat is Shoulder of Mutton 1 (beechwood) with its nearby downland samples (Shoulder of Mutton 2 to 4). The situation at Shoulder of Mutton 1 has changed considerably in recent years. The collection reported was made by A.J.C. and Dr P. M. Sheppard in 1951, when the beechwood had very little but beech litter in it except at the south end where there were some nettles, and live snails were abundant. A year or so later, a few observations were made on the grassland nearby; more than twenty-five snails were seen of which only a quarter at the most were not yellow. The wood had not changed much in 1954 (Williamson 1959). Since then cattle have been kept on this down and have trampled the ground in the wood. When it was revisited in 1960, no live snails at all were seen, and only twelve dead shells were picked up after much searching. Cattle will stand for long periods in the shade of trees and bushes, frequently moving their feet, and gradually transforming the ground to a thick clayey mud-paste in which no snail could survive long. It is quite possible that the colony in Shoulder of Mutton Wood is now extinct, but some members may have moved out a few yards into the nearby downland which is far less affected; meanwhile the background inside the wood has become greener since the cattle were removed, nearly as green as at Dean Windbreak 2. If the original population had persisted, it would by now be in complete disharmony with its background, but presumably in process of modification by visual selection to fit it.

At Pickledean there is a high proportion of pinks, which agrees well with the background, but this locality requires further discussion (p. 42). The only other dense beechwood in the non-five-banded area is Rockley Down Windbreak (Rockley Down 1 and 2), since Dean Windbreak is narrow (about 20 m wide) with an almost wholly green background at ground level. (Very few snails can be found in the three beech clumps at Sharpridge.) Although the composition of the Rockley Down Windbreak samples seems appropriate in its low proportion of yellows to a beechwood background, there are few pinks and a very large number of browns; and as the nearest downland samples, Dean Bottom 1 and 2, show between 40 and 70% browns, an area effect producing an excess of browns is indicated, and the wind-break samples cannot be used as evidence for visual selection (even if in fact they do show it).

Most of the other habitats in the non-five-banded area, apart from the area of excess browns, are grassland of various sorts, rough herbage, hedgerows or open woodland, in all of which a fairly high proportion of yellows is expected, and in nearly all is found (figure 9). It is rather lower than would be expected from figures 7 and 8 at North Delling 6, Sharpridge 2, Barton 4, Shoulder of Mutton 4 and Parsons Penning 6, and rather surprisingly high at Dean Windbreak 2. At Sharpridge 2, which has been studied intensively, there are large drifts of wind-blown beech litter from the nearby clump, which make the background redder than might be expected from the nature of the vegetation there. However, both this and Dean Windbreak 2 have peculiar features which require special discussion (p. 47 below). The high proportion of yellows can be used as evidence for visual selection only near to Shoulder of Mutton, since elsewhere we are either unable to assert that there is not an area effect or fairly sure (in the district between Rockley 3 and Monkton Down) that there is one. The proportion of yellows in the three dense mixed deciduous woods, Totterdown 4, Barton 2 and Barton 3 is much higher than would be expected from figures 7 and 8. However, at both the Barton localities there is a mosaic of patches of dense mixed deciduous woodland, and open grassland, with neither type predominating. It is not surprising, therefore, that the percentage of yellows in these two should be intermediate between those expected for the two types of habitat. This explanation, however, will not apply to Totterdown 4, which is a dense mixed deciduous wood about 150 × 180 m, compact, with little herbage, and much leaf-litter on the ground. The background is very similar indeed to that in mixed deciduous woods in the Oxford district which have a far lower percentage of yellows (figure 7 and Cain & Sheppard 1954). It is therefore possible that the area that includes the Monkton Down (1E), Totterdown (3D), Temple (3E), Rockley Down 3 (4F), Dean Windbreak (4G) and Preshute Down (4H) localities has a general excess of yellows. In proportion of yellows, the samples in area *C* are in agreement with their backgrounds or show some excess of yellows, except Smeathe's Ridge 4 (6H), which is too pink. At Combe Down 4 to 6 where visually one would expect yellows, a thrush stone sample (Combe Down 4) shows a significant excess ($P < 0{\cdot}01$) of pinks over two samples (Combe Down 5 and 6) taken only 20 m away. In this locality, then, visual selection is acting in the expected direction. Consequently, we cannot say whether the very high frequencies of yellows in the Combe Down area are due solely to visual selection or to this and an area effect. The Barbury Road 2, 3, 5, 6 and 9 localities are intermediate, but definitely too pink; the other samples in area *B* match their background well in colour as on the whole they seem to in area *D* (figure 11). Rockley North 1 was a beechwood until about 1942, but was then cut down and is now overgrown with elder bushes and nettles. The composition of the sample, as judged from that of the other Rockley samples, agrees more or less with its present type of vegetation. However, its proximity to Rockley North 2 and 3 suggests that there may be a slight area effect increasing browns here. If so, this has disappeared 450 m away at the Cemetery samples (7E). The other samples from area *D* agree in proportion of yellows with the background to some extent, the hedge at Maizey Down 4 having the fewest yellows and the more open Maizey Down 1 to 3 and Cemetery samples having more (compare figure 7).

It appears, then, that on the Marlborough Downs, visual selection is either unable to work because of a lack of choice in phenotypes (e.g. absence of five-bandeds over a large area) or seems able to disturb the area effects only slightly, as at Totterdown 4 (3D) or Fyfield Down 2 (4D), where a choice is available but the visually favoured phenotype is in low proportions. In three subareas, Fyfield Down 2, Rockley North 1 and Combe Down 4 to 6, we have sufficiently large samples from thrushstones and from the populations around them; no significant difference appears at Rockley North 1, but in both the others visual selection appears to be acting, and in the expected direction. However, good agreement between composition of sample and background is seen at Rockley, Shoulder of Mutton, and perhaps Maizey Down.

4. *Ratio of unbandeds to bandeds in different colour classes*

In the class of brown shells, there is a general deficiency of banding so that brown-banded shells are very uncommon (Cain & Sheppard 1954; Cain *et al.* 1960). In yellows and pinks no such overall deficiencies have been detected, but the ratios of banded to

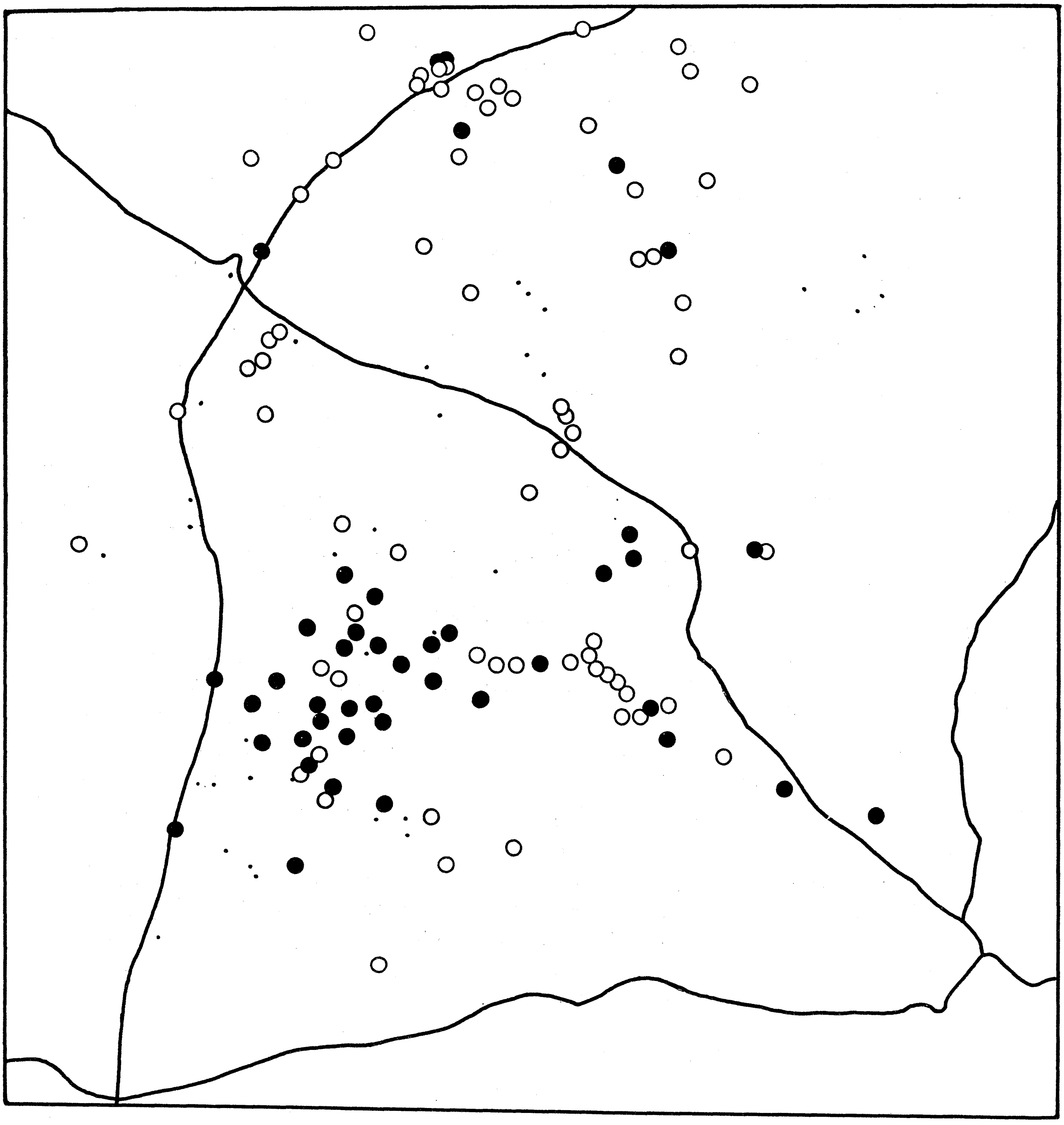

Figure 12. Cross-product ratio (yellow 00000/yellow bandeds) × (pink bandeds/pink 00000) for samples of *C. nemoralis* on the Marlborough Downs. Black circles, c.p.r. greater than 1; white circles, c.p.r. less than 1. Dots indicate localities in which no value can be obtained because of the absence of either one colour or one banding class.

unbanded shells in these two colour classes are often different within a population. The difference is best expressed as the cross-product ratio (c.p.r.) (Y00000/Ybanded) × (P banded/P00000). It will be seen from figure 12 that there is some area effect in this ratio on the Marlborough Downs, despite the fact that we have included in this figure several samples with a total of yellows and pinks less than 21.

When figure 12 is divided by vertical and horizontal medians, there is found to be a highly significant heterogeneity between the resulting quadrants in respect of the numbers of black and white circles (P slightly greater than 0·001). In the centre and north the ratio is almost always less than 1. The apparent exception at Sharpridge 1 rests on a single shell with what could be an imperfect mid-band. If it really is an unbanded, then this colony is not exceptional. In the south there appears to be a western area with c.p.r. greater than 1; elsewhere the distribution of ratios is patchy.

A ratio greater than 1 is producible either by a relative excess of yellow unbandeds or a deficiency of yellow bandeds, or excess of pink bandeds, and nothing can be said merely from inspection of the ratio about what sort of selection is acting.

Cain & Sheppard (1954) have pointed out that when yellow shells are at a visual disadvantage, they tend to have a higher proportion of five-bandeds than do the pinks in the same population, since a yellow five-banded shell is likely to be less conspicuous than a yellow unbanded. A similar but more extensive use of banding to camouflage a conspicuous shell has now been demonstrated by Clarke (1960) in *C. hortensis*. This explanation will not serve for the western half of the Marlborough Downs since five-bandeds are very rare or absent there; moreover, the edge of the area characterized by a c.p.r. less than 1 occurs within the non-five-banded area, not at its edge, and runs into the intermediate area. There is no correlation between c.p.r. and habitat either in the non-five-banded area or elsewhere on the Marlborough Downs, nor indeed one between 00300 and habitat although one might perhaps expect that in the area without five-bandeds, mid-banded might act as a rather inefficient substitute for five-banded. This finding accords with the demonstration by Cain & Sheppard (1954) and Lamotte (1951) that the visual selective value of mid-banded is close to that of unbanded. There is perhaps a slight correlation between percentage mid-bandeds in the non-brown class in this area and both locality and percentage of browns, but as percentage browns are associated with locality these two may in fact be the same.

It appears, therefore, that there is a strong area effect in c.p.r., which is not correlated with habitat. It must involve some interaction between the loci for banding and shell colour, and in the non-five-banded area this interaction must be between G and B in populations saturated with the modifier M^3.

V. Stability of the Distributions

1. *Observed stability*

Since most of the populations mentioned in this paper are reported for the first time, there is no historical evidence of stability in their phenotype frequencies. However, a few have been observed over a period of about 10 years. Samples and dates of sampling for these populations on the Marlborough Downs and for a few others from elsewhere are given in table 2. (The small 1960 sample from Shoulder of Mutton 1 is inserted for completeness but is made up of dead shells, the post-mortem ages of which are unknown.) In none of these colonies is there any suggestion of large changes in phenotype frequency. In addition, Rockley 1 and 2 have been re-examined several times between 1950 and 1956 (by A.J.C. and Dr P. M. Sheppard) and no obvious changes were noted there. Dr B. C. Clarke informs us that there is also a good agreement between collections of *C. hortensis* made 10 years apart (1949, 1959) at Silbury Hill, which is $1\frac{1}{2}$ km from the edge of the Marlborough Downs. The proportions of the unusual banding varieties of *C. hortensis* in three collections from Oare Hill (6 km south of the Marlborough Downs) reported in table 2 agree well with those reported by Hurst (1917). Hurst, like most collectors in Wiltshire, was primarily concerned with recording new occurrences of species and varieties, and the record just quoted for Oare Hill is the only one we have that gives any indication of frequencies. Records for Wiltshire are summarized and discussed by Heginbothom (1946, 1948) and Hurst (1917). The earliest authors confused or did not distinguish between *C. nemoralis* and *C. hortensis*. Several authors comment on the abundance of *C. hortensis* along roadsides and nearby downland in Wiltshire, and indeed at the present day it is extremely abundant along the Kennet and Og valleys. By contrast some record *C. nemoralis* as uncommon, but it seems that they did not search far on the downs, or may have done so in unsuitable weather (see p. 4). The latest and most accurate list (Heginbothom 1948) records both species as 'abundant'—i.e. appearing over almost the whole of Wiltshire.

In general, there is remarkably little change in phenotype frequencies in all those populations of *Cepaea* that have been investigated over a long period in localities that have not been grossly disturbed. Goodhart (1956, 1958) has reported such stability in several English and French colonies over periods of 64, 47 and 42 years. Clarke & Murray (in preparation) have shown remarkable stability of the phenotype distributions in many populations of *C. nemoralis* on sand dunes at Berrow, Somerset originally collected and mapped by Captain C. Diver in 1926, although some significant trends due to selection can be detected there.

It seems reasonable, therefore, to treat the phenotype distributions we have found as stable (that is, not fluctuating greatly from year to year) and to include some samples in our tables (e.g. some of the Rockley populations) that were taken several years before the majority. However, in all areas where there are sharp clines our samples are effectively contemporaneous.

2. *Extreme restriction of range in the past*

We have been fortunate in obtaining the following statement from Dr E. L. Jones, Department of Agriculture, University of Oxford, on the agricultural history of the Marlborough Downs. It is known that the Downs have been more extensively ploughed up in the past than at the present and it may well be thought that ploughing might have left only a few isolated colonies, and the present pattern of phenotype frequencies has resulted from a subsequent spreading out from these. The downland pastures, moreover, are affected by drought, in some years severely, and this too might have had its effect. He has kindly undertaken an investigation of these points.

* * * *

Land utilization changes and weather conditions on the Marlborough Downs ca. 1500–1960: *the possibility of catastrophe to the* Cepaea nemoralis *population*

(By E. L. Jones)

A search was made in printed and MS. sources for historical evidence bearing on the possibility of environmental catastrophe to the *Cepaea* population of the Marlborough Downs. In particular, the chances that *Cepaea* has at some date been reduced to colonies of a few hundred individuals each, isolated on remnants of downland grass, were investigated. Only two expansions of the arable acreage were considered remotely likely to have produced such a result, those during the Napoleonic wars (local climax *ca.* 1813) and the mid-nineteenth century (local climax *ca.* 1870). It is known that neither of the world wars had this effect.

Apart from these potential threats to the *Cepaea* habitat, the proportion of the Marlborough Downs under the plough has fluctuated widely throughout the past three centuries. The area suitable for *Cepaea* will have expanded and contracted about an unploughed 'skeleton' of downland grass on the escarpment, the interfluves, and the sarsen-covered fields. The last have been steadily reduced by the removal of sarsens for building purposes. It seems probable that rather less of the potential *Cepaea* habitat was disturbed on these downs by intermittent paring-and-burning and cropping during the eighteenth century than would have been affected in this way on lower, less accidented downland. There is a conspicuous absence from maps of the Downs proper of burn-and-bake locality names, which elsewhere indicate burning of the pared turf prior to cropping. The present 'core' areas suitable for *Cepaea* will not have been separated or gravely reduced unless this happened at the peak extensions of the arable acreage about 1813 or 1870. Normally the grazing pressure, mostly of sheep, will have been very great, producing the bowling-green sward described by Aubrey (*ca.* 1660) which was presumably in the main sheep's fescue (*Festuca ovina*) and red fescue (*F. rubra*).

The Napoleonic war period was marked by an unprecedented cultivation of sheepdown, which had among its results the extinction of the Great Bustard (*Otis tarda*) as a breeding species in Wiltshire. Although the downs near Marlborough were certainly affected by the extension of tillage up their sides (Southey 1951), the more remote Wiltshire downland seems to have escaped the full force of the 'reclamation' movement which was apparent in other light-soiled uplands (Davis 1811; Simond 1817). At least the higher ground and the steeper slopes of the Marlborough Downs were not broken up at this period and were good downland sheep pasture after the wars (Davis 1811; Cobbett 1912; Merewether 1851). It is not possible to argue from this to the history of particular parcels of sheep-down, many of which were at one time or another pared-and-burnt, cropped, and slowly reconverted to 'permanent' grass.

After the Napoleonic wars there was a recession of the arable acreage, although this was neither so great nor so prolonged as is usually allowed. Further advances of cultivation soon followed, with a noteworthy burst of activity in Wiltshire once farm costs had been lowered by the Tithe Commutation Act of 1836 (Caird 1852). This extension of ploughland reached peaks between the early 1850's and early 1870's, when in some years farmers 'would plough and grow mangold-wurzel on their fathers' graves' (Hughes 1859). The tithe maps and schedules for the relevant parishes show that only the escarpment face and a few fairly small patches such as Barton, Manton, Rockley, and Barbury Downs remained uncultivated by the years 1839 to 1848, when for instance arable fields reached right to the base of the earthworks of Barbury Castle (Tithe Records, 1839 to 1848). In 1849 the plough was still encroaching on many of the Marlborough Downs earthworks (Merewether 1851). With important ploughing 'campaigns' like that of the Crimean war to come, the area available for *Cepaea* during the mid-nineteenth century was with little doubt smaller than in 1960.

Summer droughts with serious repercussions on agriculture, such as high mortality among downland sheep flocks and the destruction of root-crops, are known on good evidence—some of it from Wiltshire—from the late seventeenth century onwards (Capps 1713 to 1774; Baker 1883; Cobbett 1912; Johnson 1931; Ashton 1959). Grass on thin soils over solid chalk is usually free from serious parching, but Wiltshire down pasture 'burnt-up' in some years, for example, 1870 and 1874 (Baker 1883). *Cepaea* are presumably able to aestivate through droughts which are severe by these agricultural standards, of which there have been several in each century, but the occurrence of notable summer droughts, in 1864, 1868, and 1870, at the period of maximum arable acreage, must be recorded. There were, however, wetter seasons between these years which would have given the *Cepaea* population time to recover, if indeed drought had much reduced it.

The information on the past utilization of the Marlborough Downs strongly supports the view that at no time during the nineteenth century would the escarpment face, the sarsen fields, Wroughton and some other copses and some steep grass slopes and downs used for sport have been excluded to *Cepaea*. There is no evidence or reason to suppose that the present core areas of the *Cepaea* forms were separated by cultivation, especially as the escarpment would form a continuum linking them. It must be acknowledged that the available area has fluctuated and was smaller in the mid-nineteenth century than now, and that droughts may have lessened *Cepaea* numbers during this period, but this presents no case for the isolation of small colonies.

* * * *

It would appear, then, that we have good evidence that on these Downs there has always been an area of grassland untouched by the plough, running along the highest parts and connecting together all the areas which we have defined by phenotype frequencies. The probability of tiny colonies, one for each area, being completely isolated from each other therefore is slight. Moreover, ploughing, especially in the past, would not have destroyed woods nor field boundaries and hedges of which indeed there may have been many more than nowadays (after the introduction of barbed wire). Equally small is the likelihood that drought years have been responsible for producing conditions under which sampling drift could be important. These snails can live for several years, and when buried can resist many months of unfavourable weather.

3. *Subfossil* Cepaea

There are no records of fossil or subfossil *Cepaea* from excavations on the higher Marlborough Downs, but there are several from elsewhere in Wiltshire, including four sites very close to the district, namely, the Sanctuary (SU 118679, by the southernmost locality for *Cepaea* in figure 2), Avebury (SU 103700, 2 km west of Parson's Penning 6, 2C), Silbury Hill (SU 100686, 1 km south of Avebury), and Windmill Hill (SU 087714, 3 km west-south-west of Monkton Down 5, 1E). The molluscan material from the archaeological excavations at these well-known sites was identified by A. S. Kennard, whose collections and notebooks are in the British Museum (Natural History) where we have inspected them. At all these localities we have found at the present day only *C. hortensis*, but subfossil *C. nemoralis* as well as *C. hortensis* were identified by Kennard. He, of course, did not recognize spread-banded shells as such; by comparison of his specimens with his records it is clear that he referred light manifestations of spread-banded to 00300, and heavy ones to (12345) or similar formulae, which he also used for shells without spread bands but with actual fusions. In subfossil shells the colour is seldom determinable, but the banding usually is, and in *C. nemoralis* a useful check is given by the pigmentation of the lip. If the lip is dark, but there are no bands visible, the shell is unbanded. If the lip has faded, nothing can be said (unless bands actually appear on some part of the shell).

The composition of the samples recorded by Kennard is astonishing; from the Sanctuary five unbanded, from Avebury (two separate sites) twenty-five unbanded and one (12345), from Silbury Hill three unbanded, and from Windmill Hill thirty-four unbanded. We have seen the Sanctuary and Silbury material and can add that of the Sanctuary specimens, two are browns and another not yellow (brown or pink), and of those from Silbury one is not yellow. (The remaining three are indeterminable.) We have not seen the (12345) from Avebury but from inspection of Kennard's other material it could be either (12345) or heavy spread-banded.

The very large number of unbandeds from these sites is most surprising. (Some bandeds were found at other Wiltshire sites.) The most likely explanation is that many of them were brown. If this was so, then it would seem that in the Neolithic (Windmill Hill, Avebury) and Bronze Ages (Silbury, The Sanctuary), i.e. from about 2500 to 500 B.C. the available evidence points to an area of excess browns, perhaps with heavy spread-bandeds, just south and west of the present area of excess browns and close to that with spread-banded, quite possibly forming an extension of these very areas. The temporal spread of these samples from Neolithic to just pre-Roman also suggests a considerable stability of gene distribution. A preliminary examination of samples from Salisbury Plain with the same time-distribution, and of modern samples from the same district supports the suggestion of stability (Cain & Currey, in preparation).

VI. The Lambourn Downs Collections

Most of these were taken in various habitats over a distance of about 5 km along or near to the Lambourn–Childrey road from where it rises up over the chalk scarp of the Berkshire downs, about 20 km east of Marlborough, to where it descends to about 450 ft. just north of Lambourn, in a dry valley tributary to the river Lambourn. The remainder are strung out along the Ridgeway to the west for nearly 5 km. The localities are shown in figure 13 and the composition of the samples in table 3. The area is of open rolling downland with something of a plateau south of the scarp face. There are some dense beechwoods and several very small clumps; Sparsholt Firs (not now notably coniferous) is a beechwood.

Most of the downland is cultivated (some only recently), except for a large gallop on the east side of the Lambourn to Childrey road, south of Boundary Covert, and another on the west side, south of Triangle Clump. Also, in the valley on the west side is a flat patch of old downland with many barrows, probably never disturbed by cultivation. The Ridgeway, an ancient downland track, runs along the upper edge of the scarp, and the colonies just south of it are either on the narrow plateau or at the heads of dry valleys running south.

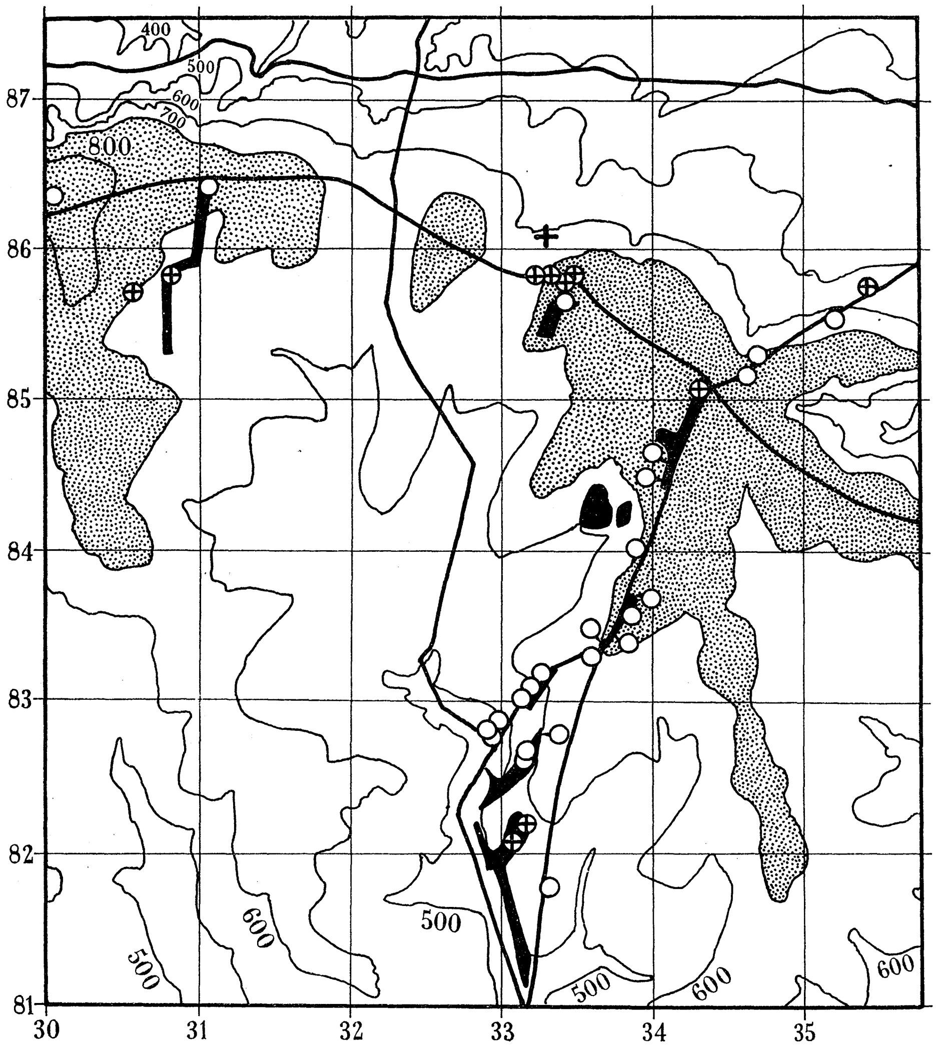

FIGURE 13. Map of the Lambourn Downs showing localities observed for *C. nemoralis* (circles), *C. hortensis* (crosses), and mixed colonies (circles with crosses). Some roads and the Ridgeway shown, also contours at 100 ft. intervals. Land over 700 ft. stippled. Woods investigated, black. Kilometre squares of the National grid shown.

Figure 14 gives the proportions of yellows and effectively unbandeds for comparison with figures 7 and 8. It will be seen at once that the proportions of effectively unbandeds are far too high over the area generally. Table 3 and figure 17*d* show that the effectively unbanded class is made up principally from high frequencies of 00300. Spread-banded is relatively common over most of the district. The samples for Sparsholt Firs 1 and Pigtrough Roadside 1 and 2, those from Lambourn Road and Dewdrop Covert 2, and those from Long Covert 2 and 3 and the Seven Barrows localities strongly suggest that visual predation is affecting colour considerably, since the beechwood samples have about 20 % yellows, and the rough herbage and open downland ones have from 58 to 100 %. Visual predation is certainly acting in several of these localities, as can be seen from the occurrence of predated shells. However, the samples from the upper ends of Dewdrop Covert and Long Covert, and those from the beechwoods at greater altitudes, namely, Old Warren, the Triangle Clumps, Boundary Covert, Clump 3 and Sparsholt Firs 2 and 3, have a considerable or even a vast excess of yellows for the nature of their backgrounds. It is true that at Sparsholt Firs 2 and 3 and Old Warren there is more green in the background at ground level than is usual in beechwoods; but the samples showing the greatest excess of yellow are on dark backgrounds. We have live shells only from Long Covert 3 and it is possible that the predated shells found in the tiniest clumps (e.g. Triangle Clump) were brought there for cracking from downland nearby; but this is not at all likely to be

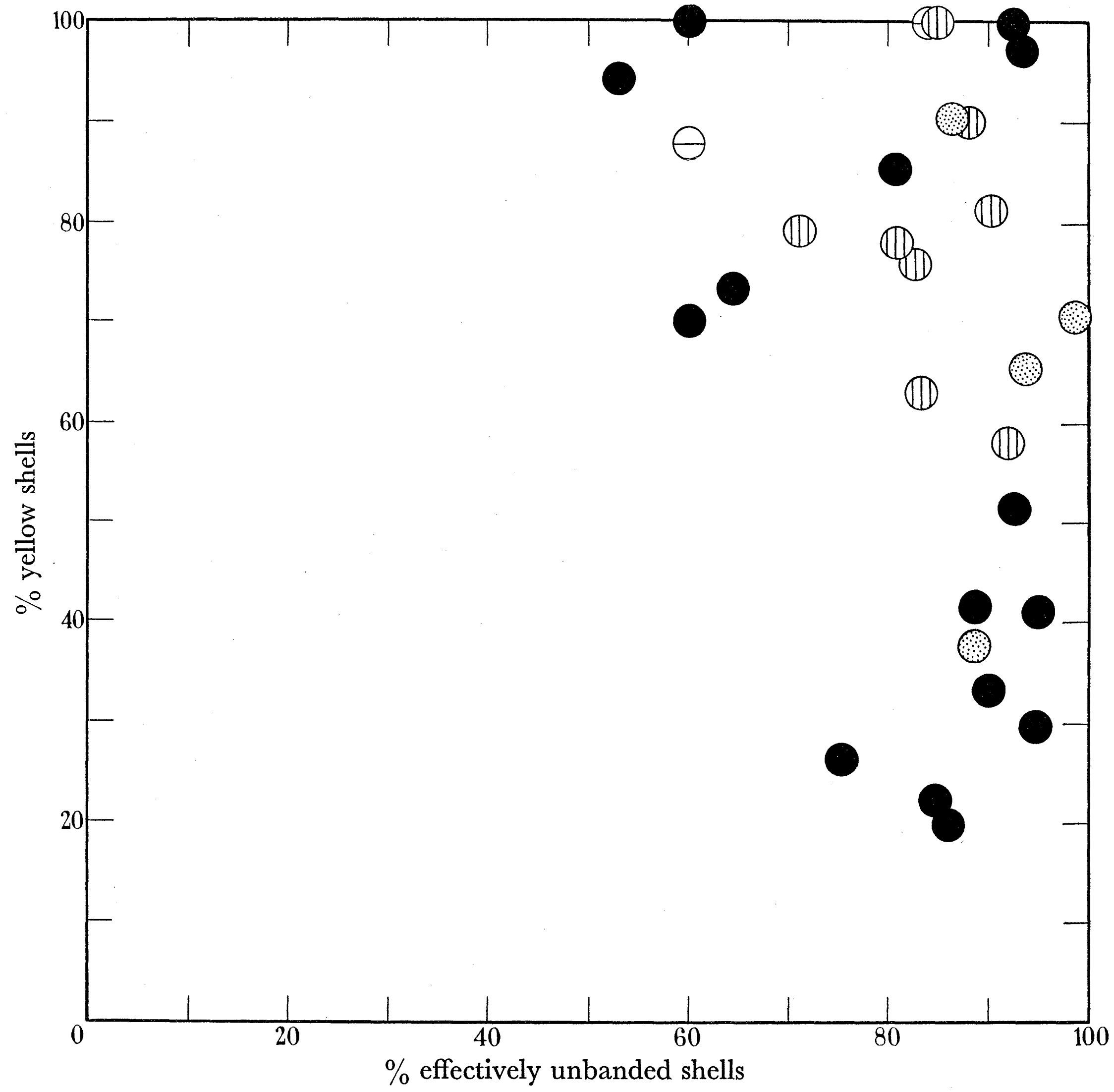

FIGURE 14. Scatter diagram (as in figure 7) for samples of *C. nemoralis* from the Lambourn Downs.

the situation in Old Warren and Boundary Covert, and probably not in others. The collections from Rams Hill Plantation 2, Uffington Down and Uffington Castle also strongly suggest visual selection, but the extreme yellowness of the samples from Rams Hill Plantation 1 and Rubblepit Plantation indicate an area of excess yellows which may well include at least Uffington Castle. It seems, therefore, that visual selection is effective on colour at the north-eastern and southern ends of this district, but in most of it there is a strong area effect producing an excess of yellows. The acme seems to be in the vicinity of the Triangle clumps and Boundary Covert, since the proportion of yellows increases with altitude in both Dewdrop Covert and Long Covert, and markedly along Old Warren, without there being any great change in the colour of the background. This area may extend northwards and westwards to include Rams Hill Plantation 1 and Rubblepit Plantation.

The general similarity between the peculiarities of the Lambourn Downs samples and those from the Marlborough Downs is striking. In both, we have a strong area effect in banding producing a great excess of M^3. In both there is an area with a great excess of yellows. And in both, areas in which visual selection appears to be effective exist, but they are restricted. (No area effect within the Lambourn district is observable in spread bandeds.) This investigation, therefore, confirms the expectation that the higher chalk downs are subject to area effects. The nearest colonies to those just described which have been investigated so far are at the edge of the scarp, namely Windmill Hill, 2 km north-east of Sincombe Farm, and Segsbury Camp, 7 km east of it. Their compositions are given in table 4. The Windmill Hill sample is from a hedgerow and agrees well with others in the same type of habitat but off the Downs. The Segsbury collection is from downland grass on the top of the inner vallum of an Iron Age fort, and contrasts strongly with grassland ones near Lambourn in being heavily five-banded. It may well indicate an area effect similar to that around Coombe Down on the Marlborough Downs.

VII. Area effects in colour and banding outside the Marlborough and Lambourn Downs

The demonstration of such remarkable area effects on the Marlborough and Lambourn Downs makes it necessary to re-examine the data of Cain & Sheppard (1954) to determine how far area effects can be seen in other districts. The map given by them (1954, p. 101) of thirty-seven colonies in a district of about 9 × 7 km including Oxford shows that here, variation between colonies is indeed correlated with differences in habitat, not at all with geographical location within the district, and the variation is what would be expected from the types of background occurring in this district, which are rough herbage, hedgerows, and mixed deciduous woods.

The scatter-diagram for these localities and for all the others within 12 miles of Oxford, including some newly reported ones (data in table 4), is given in figure 7; again it will be seen that agreement with background is good and this is almost entirely irrespective of locality. However, all the oak woods are in a comparatively small area within which no hedgerow or rough herbage colonies have been found, so that there may be an area effect in them rather than visual selection by background. Also, in two colonies close together (Rycote and Hornage Farm), there may be an excess of pinks. In the immediate vicinity of Oxford, however, the numerous colonies sampled by Cain & Sheppard provide an effective disproof of area effects involving percentage yellow and percentage effectively unbanded shells. In two other places, Pusey Common and Tackley Heath, there are samples from almost adjacent colonies on very different types of background, and the agreement with the backgrounds is so good that visual selection must be effective. (It is of course conceivable that the woodlands at these two widely separated places are each just within an area of high pinks, and the other colonies just within other areas with exactly the effects required to produce an apparent causal correlation with background; but it seems improbable, particularly as there is no evidence of strong area effects in this district, and considerable evidence of variation with background.)

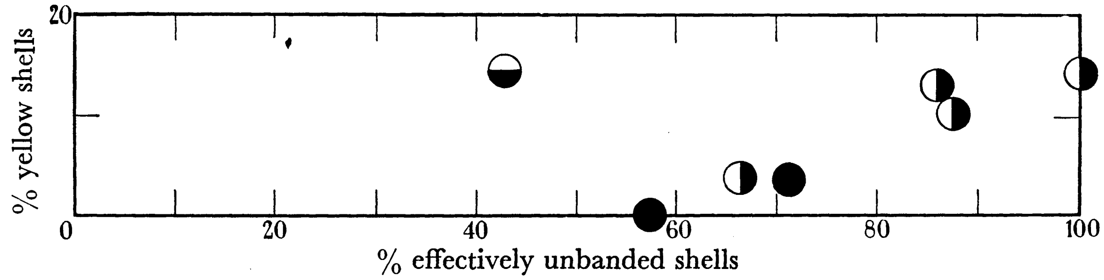

Figure 15. Scatter diagram (as in figure 7) for samples of *C. nemoralis* from the Savernake–Hungerford district.

In figure 15 are shown the colonies from the Savernake–Hungerford district, which include the rest of our samples from oak woods. Unfortunately, the other samples in this district are also from woodlands, but from both mixed deciduous and beech woods. By comparison with figure 7 it will be seen that there is a good general agreement with woodlands in the Oxford district; it is possible that the resemblance in the oak woods could be due to a similarity of area effect in the Savernake–Hungerford and the Oxford districts, but there is no area effect to account for the similarity in all the woods within the Oxford district and their resemblance to those elsewhere. There is no reason, therefore, to think that samples from two groups of oakwoods 56 km apart should be similar as the result of a coincidence in area effect. Figure 8 shows a number of samples distributed widely in Britain, though not on chalk, and these also, as far as can be judged from their backgrounds and the similarity of their composition to those on the same backgrounds in the Oxford district, show little evidence of area effects; Bredon Hill Wood (the beechwood with most yellow in figure 8) is discussed below.

The correct assessment of the selective forces acting in beechwoods and on downland is a matter of some difficulty. On the one hand, all our beechwood samples (except a few in the Lambourn district, already discussed, and that on Bredon Hill) show a remarkable similarity (figures 7 to 9, 11, 15 and 16) and precisely the composition (of percentage yellows and percentage effectively unbandeds) that one would expect to be produced by visual selection; and they are widely distributed from Pulpit Hill near Princes Risborough (Chilterns) to Ford (west Wiltshire), a distance of 100 km, and north to Trafalgar Wood, north-east of Cheltenham. However, for none of these beechwood samples, except on the Marlborough and Lambourn Downs, do we have samples from hedgerows, rough herbage, or downland immediately adjacent, so that they suffer under the same suspicion as do our oakwood samples; but they are far more widely distributed. Nevertheless, all except

Ford and Trafalgar Wood (limestone uplands) are on chalk downs, and we know from the Marlborough and Lambourn districts that area effects can occur on downland, and change abruptly over small distances.

However, at Shoulder of Mutton, and at Rockley, we have good evidence of visual selection for colour in beechwoods, and the resulting composition is so like that shown by all our other beechwood samples scattered over such a distance, that it seems far more likely that visual selection is determining their characteristics. This conclusion is supported by a consideration of the Bredon Hill samples (on limestone). The beechwood is a very steep and narrow one, and its sample shows a high proportion of yellows and of banding, but that from Bredon Hill Grass, only 110 m away, shows a far higher proportion of yellows, as would be expected if visual selection were important there. Moreover, only in the wood have browns been found, and considerable thrush predation is occurring at both these localities.

Figure 16 shows the composition of all our downland samples from outside the Marlborough and Lambourn districts. Beechwoods and mixed deciduous woodland samples resemble those from the same habitats elsewhere, except that some of the mixed deciduous woodland samples are rather yellow. The diversity within the short turf and long grass categories is surprising. One would certainly expect, after seeing the good matching with background in other categories, that samples from green backgrounds (long and short grass) should be mainly yellow. Knoll Down and Knoll Down Roadside, 5 km west of the Marlborough Downs, have a high proportion of browns and spread-bandeds (table 4), and probably no true five-bandeds; they again suggest area effects like those near Marlborough. Dogtail Down is immediately adjacent to Dogtail Plantation, a mixed deciduous wood from which the sample appears to be what one would expect. The downland 30 m from the plantation has nothing remarkable about it, but the sample seems to contain only four sorts of chromosome, namely $(G^{DP}B^{0})$, $(G^{DP}B^{B})$, $(G^{PP}B^{B})$ and $(G^{DY}B^{B})$. The sample is also saturated with M^{3}. This relative paucity of genetic variation on the downland as compared with the nearby woodland sample suggests a small colony begun from a single individual, which might explain the absence of five-bandeds; but the remarkably high proportion of pinks, as high as in the wood, could point to an area effect involving both the wood and the downland. The Chirton and Water Dean Bottom samples and those from Dogtail Down and Dogtail Plantation are within an area on Salisbury Plain about 6·5 km long and 1·5 km wide. Together they suggest an area effect producing a high proportion of M^{3}. Beacon Hill Fort, between Whitchurch and Newbury, is well banded but with far too many pinks. This sample is of predated shells, almost all thrush-predated. It may well be thought that there is an area effect here producing pinks, just as at Fyfield Down 2 there is one producing an excess of browns, although thrushes are predating there and favouring yellows. In sample 1 from King's Play Hill (5 km south of Calne, Wilts.) there is a surprising number of browns with five bands all fused, many pinks, and very few yellows. The small sample 2, lying only 100 m away, resembles sample 1 except that it contains five shells with hyalozonate banding, which greatly increase its proportion of yellows. Hyalozonates are rare in *C. nemoralis*, and we have found them on the downs only here, at Coombe Down (Marlborough Downs), the Pentridge (Dorset) and very rarely elsewhere.

The samples from Crowell Hill (Chilterns), Aston Tirrold (Berkshire Downs), and Kimpton Down and Thruxton (Salisbury Plain) all agree in having far too few yellows, and all are too pink except Aston Tirrold (too brown). These are the colonies that Cain (1953) suggested were influenced by tone-predation by rabbits.

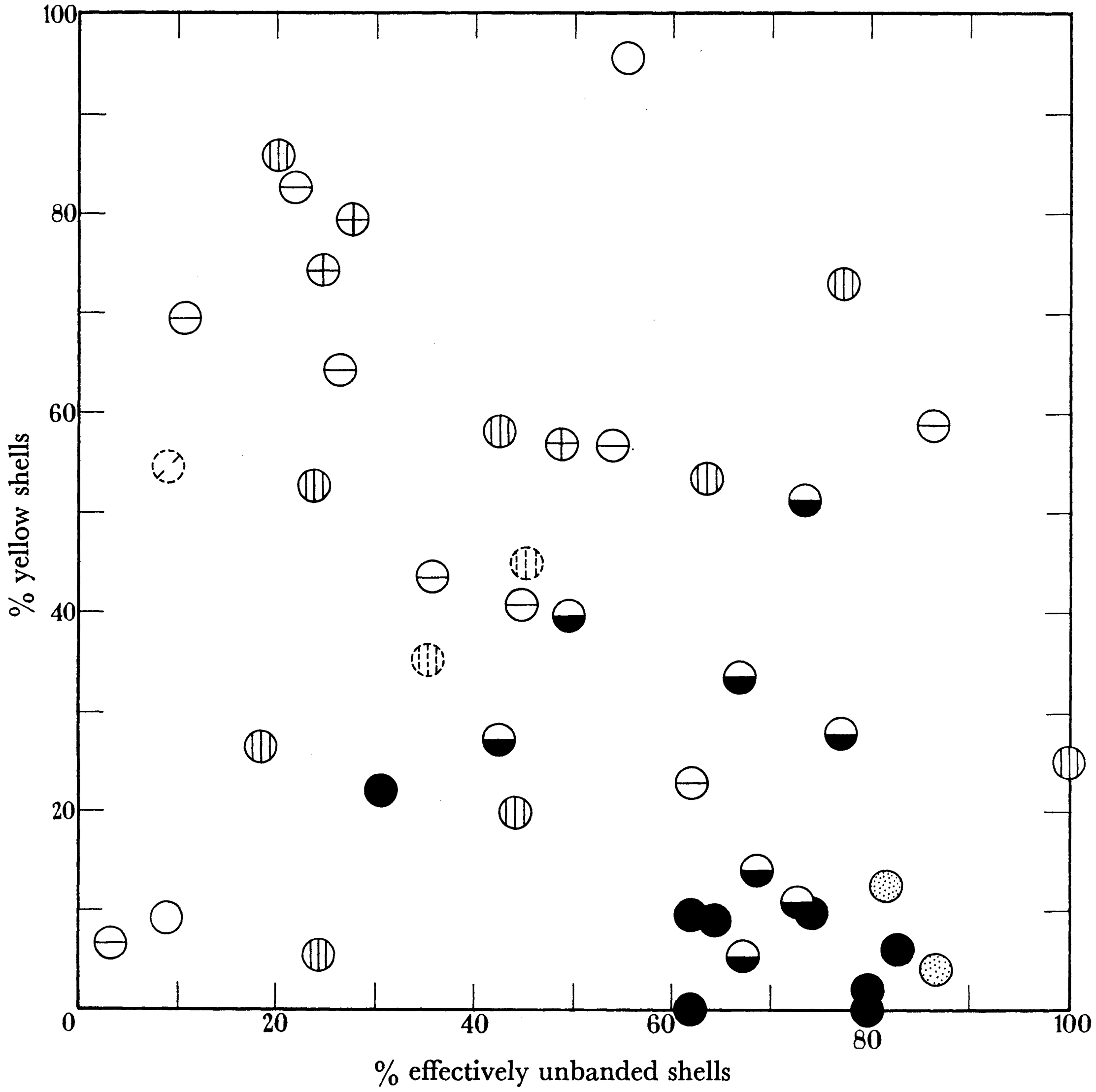

FIGURE 16. Scatter diagram (as in figure 7) for samples of *C. nemoralis* from all our localities on the Chalk apart from the Marlborough and Lambourn Downs.

The remaining grassland samples in figure 16 are very scattered geographically, and how far area effects are responsible for the composition is unknown except at Wittenham Clumps, where we have samples from closely adjacent mixed deciduous woodland, downland, and rough herbage, all of which show proportions of yellow and effectively unbandeds that would be expected from visual predation in relation to backgrounds. Wittenham Clumps is on chalk, but this is only a small outlier left on a large plain of Jurassic rocks.

The contrast between the lack of area effects in localities away from downland, and their importance, certainly on the Marlborough Downs and probably in several other downland districts, is remarkable.

VIII. Significance of the area effects

1. *Probable causes of the area effects*

It is clear from § IV that the remarkable area effects found on the Marlborough Downs cannot be accounted for by visual selection. Random variation produced by sampling drift or the founder effect has been frequently put forward as an explanation of the differences between colonies. That *Cepaea* occurs in populations readily isolated by small distances would incline one to suspect that it should be particularly good material for demonstrating sampling drift. However, the geographical distribution of the phenotype frequencies on the Marlborough Downs is sufficient to show that sampling drift is not the present cause of the area effects. If it were, one would expect to find not whole areas sharply characterized by absence or excess of particular phenotypes, but a random scatter of colonies with an excess interspersed with others with a deficiency. Lamotte (1951) and Schnetter (1950) have shown that colonies of more than about 40 m diameter cannot be considered as panmictic, and it is evident that such an area as the non-five-banded one cannot be considered as containing, in effect, one population.

Sampling drift, therefore, is not the agent determining the distributions of frequencies at the present day, and, as shown in § V 2, there is no reason to believe that in the last few hundred years there has been a catastrophe sufficient to destroy the *C. nemoralis* populations on the Marlborough Downs on such a scale as to leave only a few widely separated and tiny groups, in which sampling drift could occur. There remains the possibility that there have been climatic changes sufficient to cause *C. hortensis*, at present mostly in the valleys (§ VIII 2), to spread up the slopes and over the higher downs, restricting *C. nemoralis* to a few localities. However, the resulting populations would have to be sufficiently numerous and peculiar to produce the following: a predominantly brown and non-five-banded population spreading from the Overton Down area or nearby; a mainly yellow population lacking both five-bandeds and browns spreading from somewhere to the north of the first; one almost entirely five-banded spreading over the north-eastern area; two or perhaps three producing different associations of colour and spread-banded in the south, and all by a remarkable chance without five-bandeds. To these must be added further populations to account for the combinations of excess browns and low cross-product ratio around Dean Bottom as well as the excess browns and high ratio around Overton Down; and excess yellows and high ratio in the south of the excess yellow area as well as excess yellows and low ratio further north. Moreover, all of these populations except the north-eastern must be saturated with M^3.

Regrettably little detailed information is available for the Marlborough Downs in and before the Middle Ages, but we do know that Wroughton Copse was in existence well before 1773 (Andrews & Dury 1773), but after 1300. Mixed deciduous woodland in general outside the Marlborough district has between 20 and 70% of banded snails (Cain & Sheppard 1954), and if there has been a restriction of range since 1773 with Wroughton Copse remaining as a refuge in the Overton Down–Clatford Down area, it is most surprising that this area has no five-bandeds. If the restriction took place before this, then it is surprising that the area effects should still be so marked.

Moreover, *C. nemoralis* is a common and often abundant snail in many different types of habitat on moderately or very calcareous soils all over England and Wales, and indeed from Denmark to the Pyrenees. It is able to exclude *C. hortensis* from one rather extreme habitat (sand dunes) in Britain (Taylor 1914).

While the hypothesis of restriction of range through competition cannot, of course, be disproved, it seems to be highly unlikely. And the evidence of the subfossil *Cepaea* (§ V 3) is in favour of the phenotype frequencies being highly stable over thousands of years.

It seems then, that the most likely hypothesis is that the area effects are produced largely by selection, and have been stable over a very long period. It is usually much easier to show that selection of some sort is acting in the wild than to identify the agent responsible for it, still less the details of its action. However, we have two clues to the sort of selection acting, provided by the relative distribution of *C. nemoralis* and *C. hortensis*, and the general geographical distribution of the colour morphs in *C. nemoralis*.

2. *Distribution of* C. nemoralis *and* C. hortensis

C. hortensis ranges much further north than does *C. nemoralis* (Taylor 1914), being found in the north of Scotland and Iceland (and in Labrador), while *C. nemoralis* goes no further than the southern half of Scotland. In southern England, colonies of *C. nemoralis* and *C. hortensis* are often closely adjacent, and mixed populations are not infrequent although not common. In the Marlborough Downs area, however, there is a remarkably clear pattern of distribution of the two species; *C. hortensis* predominates in the valleys and on the low plain at the foot of the scarp, while *C. nemoralis* is widespread on the uplands. This distribution is shown in figure 2. Where the ground rises steeply, the changeover from apparently pure *C. hortensis* to pure *C. nemoralis* can occur over very short distances; it takes less than 25 m at Barbury Road. Rather greater distances are taken at Sharpridge 4, Monkton Down, Coombe Down, Uffcott Down, Walker's Plantation, and along the Winterbourne Bassett road from Berwick Bassett 1. There are scattered colonies of *C. nemoralis* on the Lower Chalk plain, especially to the north of the district (Wroughton South, Burderop Wood, Hackpen Copse hedge, Chisledon Camp corner, and south-west of Wroughton airfield) but close to the foot of the scarp there is a vast preponderance of *C. hortensis*. *C. hortensis* preponderates also along the Og and the Kennet valleys; indeed, there is no reason to think that *C. nemoralis* occurs in them at all, while *C. hortensis* is abundant. The *C. nemoralis* area on the Marlborough Downs is therefore cut off to the west, south and east, and probably has only very restricted gene-flow from the north. *C. hortensis* also predominates along the tributary valleys opening into the Kennet and Og, namely, Clatford Bottom, Barton Bottom, the valley leading into Ogbourne St Andrew, and the large valley running up north-westwards into the centre of the Downs, with extensions up Temple Bottom, Wick Bottom, and Dean Bottom. Cultivation is extensive in this area, but *C. hortensis* is certainly abundant in Temple Bottom and up its sides, and up as far as the lowest part of Rockley North 2 in the Dean Bottom branch, and in Rockley village, and at the foot of Rough Down. Some *C. hortensis* extend up into the Rockley colonies, at Rockley 1, 2, 9, Rockley North 4 and Clatford Down 6, and it is predominant at Barton 4, 8 and 9. It is not uncommon at the Cemetery localities, and a few occur at Maizey Down 4.

In general, *C. hortensis* is far more abundant in the valleys and around the foot of the scarp than elsewhere, reaching to about 680 ft. in Clatford Bottom and on Overton Down and 700 ft. in Temple Bottom. As the soils along the valley bottoms are mainly alluvium and gravels, and those around the scarp foot and on the valley sides derived directly from the chalk, there is no association of this species with a particular soil type in this district. When it appears at higher altitudes it does so in strict association with trees, namely at Maizey Down 4 (836 ft.), Smeathe's Ridge 1 (880 ft.), the lower end of Shoulder of Mutton (750 ft.), the area south of Monkton Down 1 (*ca.* 870 ft.) and the Totterdown area (820 ft.). Only two occurrences have been noted on the high downs in an open habitat without trees or bushes, namely, Sharpridge 3 (870 ft.) and Monkton Down 1 (875 ft.), but the former is very close to a beech copse (about 30 m away) and the latter only a few metres from a hedge. All the other localities found above the 700 ft. contour, which more or less defines the high downland area, whether woodland, hedgerow or grassland, have only *C. nemoralis* except for a single shell in rough herbage on a bank near Clatford Down 8 (715 ft.) and one at Clatford Down 1 (750 ft.). Between 700 and 600 ft. it is still very usual to find *C. hortensis* associated with trees and shrubs and absent from the downland grass (e.g. Rockley, and Clatford Bottom).

In the valley areas in which *C. hortensis* predominates, most of the localities are in hedgerows or near trees, because of the modes of cultivation used there, but the lower slopes of Rough Down are more open, and the species occurs on open short-turfed down at Down Barn 2 and Overton Down 7 (670 and 680 ft.) Just outside the Marlborough Downs district, at Silbury Hill (500 to 616 ft.) and Knoll Down (650 ft.) *C. hortensis* is common on open downland. Both species, therefore, in the areas in which they predominate, are found in all types of habitat, but where *C. hortensis* is found in a predominantly *C. nemoralis* area, it seems to be restricted to the vicinity of trees; this was first pointed out by Dr B. C. Clarke. This restriction suggests that competition between the two species, the mechanism of which is not known, and may well relate to food or moisture, rather than to temperature, is somewhat relaxed in or near trees and woods. However, *C. hortensis* does not occur in all woods, hedges and thornbush clumps on the higher downs above 700 ft.—it has not been found in Overton Down 6 (beechwood), North Delling 3, Totterdown 4, Berwick Bassett 1, Sharpridge 1, the beech clump by Sharpridge 2, Coombe Down 1, Dean Windbreak 1 and 2, Rockley Down 1 and 2, and Barton 2 and 3. It occurs only at Maizey Down 4, Smeathe's Ridge 1, Sharpridge 3, Shoulder of Mutton 1, Monkton Down 1 and 6, Glory Ann Barn (close to Monkton Down 1), Totterdown 3, and Wroughton Copse. Moreover, in Rockley North 2 and 3 (beechwood), it occurs only at the lower altitudes, near the road, and the same is true of Rockley 1 and 2. At Shoulder of Mutton Wood also, it was certainly most abundant at the lower end, and probably restricted to it. In fact, all three of the woods that slope considerably from one end to the other and have *C. hortensis* show this species as confined to or most abundant at the lower end.

That *C. hortensis* ranges so much further north than *C. nemoralis* suggests that it is able to withstand colder conditions, which may be expected to affect these animals more in summer, when they are active; certainly the distribution of isotherms in Britain (Bickmore & Derry 1958) would suggest that it is the summer temperatures, the isotherms of which run across Britain from east to west, that limit *C. nemoralis* rather than the winter ones, the isotherms of which run the length of Britain from south to north. The Marlborough Downs area is far too small for broad climatic differences to occur, but it is very well known (Bilham 1938; Geiger 1959; Manley 1952) that considerable differences of climate can occur over distances of sometimes only a few yards because of local topographical features. These differences are produced mainly by cold air draining down from higher land on still, clear nights, and forming cold pools and rivers covering the bottoms of nearby valleys. This effect can be considerable (Geiger 1959) and indeed spectacular, even under the mild Atlantic conditions of Britain, as is well demonstrated by the famous frost-hollow at Rickmansworth (Hawke 1944, see Manley 1952). This effect develops most strongly in the least wooded and most open country, and in country with expanses of rolling upland cut into by well-marked valleys. Hedges and other obstructions following the contours can act as barriers, damming back the downward flow of the cold air and decreasing the effect. Of all the main types of country inhabitable by *Cepaea* in southern England, the larger expanses of open downland should show this effect best; as a consequence it might be expected that on downland there would be a strong local separation of more northerly species from others except where competition between them appears to be reduced. There appears, therefore, to be a good agreement between the observed distribution of the species in the Marlborough Downs area with the more northerly range, namely *C. hortensis*, and the probable distribution of low temperatures during the active season of these snails.

3. *Distribution of brown in* C. nemoralis

If the distribution of *C. nemoralis* on the downs is correlated with local climate, and if the broad geographical distributions of its morphs suggest that any of them have distinct climatic preferences, then it might be expected that in the Marlborough district the more northerly morphs of *C. nemoralis* should be abundant where a local climate prevails that is cooler in some respects. Although much has been written (Schilder 1950) of the geographical variations in distribution of the morphs of *C. nemoralis* the data are in general insufficient for firm conclusions to be drawn; however, it is known that dark browns are rare in France (Lamotte, personal communication; examination of the Locard Collection, Musée d'Histoire naturelle, Paris, by A.J.C. and B. C. Clarke) but common in northern Europe including the British Isles. This distribution seems to indicate that dark browns are better able to withstand cooler summers. The distribution of the brown phenotype on the Marlborough Downs is shown in figure 6. High frequencies are certainly associated broadly with the short and low-lying valleys opening into the Kennet valley, or with the lower ends of the larger valleys running down from near the scarp face, and this would suggest some connexion with the accumulation of cold air. Two facts seem to strengthen this supposition, namely, that the highest frequencies of brown (over 80 %) are all but one on open downland, which is most likely to lose heat (Geiger 1959), and that the area with most browns is perhaps that in which *C. hortensis* meets and overlaps with *C. nemoralis* most broadly. It is the only area in which *C. hortensis* is found on open downland on the Marlborough Downs (Down Barn 2, Overton Down 7, Clatford Down 1) except for Barbury Castle (two dead shells), another area in which browns are not infrequent, and Rough Down, where browns are common.

Without much more information about the details of local climate, no conclusion can be reached. One locality, Pickledean, does seem to be in direct contradiction to the hypothesis, but is anomalous in another respect. As one goes from Overton Down 1 to Overton Down 7 and then descends Pickledean Bottom, one passes from pure *C. nemoralis* with abundant browns to a mixed population and then to pure *C. hortensis* (at Down Barn 1 and 2), which extends halfway down Pickledean Bottom. But lower down Pickledean, remarkably enough, *C. hortensis* disappears to reappear again at the road. The only *Cepaea* found in the lower bottom, except at the road, were two pink *C. nemoralis*, and in the adjacent windbreak there is only *C. nemoralis*, moreover mainly pink, not brown. This is the only place on the Marlborough Downs where on going down a bottom or the scarp face one passes from *C. nemoralis* to *C. hortensis* and then back to *C. nemoralis*. Nothing in the appearance of the bottom suggests any peculiarity, and the disappearance of *C. hortensis* here is as inexplicable as it is surprising.

4. *Banding*

In banding of *C. nemoralis*, as well as in colour, we find remarkably steep clines, but it seems unlikely that they are related to climate. The division between the banded area *C* and the non-five-banded area *A* runs down a broad valley, separating at the Barbury gap two similar areas of high downland, and it is difficult to see how there can be differences in aspect, altitude, geomorphology, soil or vegetation between these areas that could cause so remarkable a difference in the frequency of the five-banded phenotype. It is true that the populations in the Barbury gap (*B*), where the banding cline is steepest, are remarkable for both a high proportion of pinks to yellows, and the occurrence of browns (and moreover banded browns) otherwise absent from the northern half of the downs. But in these respects the Barbury populations stand out from those around them and do not conform to the clinal pattern seen in the banding distribution. They may point to some peculiarities in the gap itself, but cannot help to explain the differences on the two sides of it.

The five-banded phenotype is altered by both the 'unbanded' and 'mid-banded' genes (B^0, M^3), and an examination of their relative frequencies in the non-five-banded area *A* is necessary. Gene frequencies can readily be calculated for this purpose from the Hardy–Weinberg formula, since although this formula assumes no selection, it is very insensitive to selection pressures below 10%, which would produce effects comparable with the sampling errors introduced in the sizes of our samples. Gene frequencies are shown in figure 17. The frequency of B^0 is seldom high ($> 0{\cdot}4$) and varies rather erratically from one locality to another, but does decrease towards the north-east and reaches very low values ($< 0{\cdot}1$) at Coombe Down and Burderop Down. The frequency of M^3, on the other hand, is 1·0 or very little less over the whole of the non-five-banded area, and drops very sharply across the Barbury gap, from 0·8 at Barbury Road 8 (41) to 0·02 at Barbury Castle 3 (41), a distance of about 450 m. Moreover, along the whole of the crescent of high down and its flanks from Barbury Castle to Coombe Down it does not rise above 0·04 and is usually 0. The frequency of M^3, therefore, characterizes the two main areas even more clearly and consistently than does the phenotype frequency of five-bandeds. However, B^0 and M^3 do occur in the five-banded area at low frequency, and offer material for selection to work on. It seems likely, therefore, that selection of some sort is keeping their frequencies low. It might be objected that no five-bandeds have been seen within the greater part of the non-five-banded area, and therefore that since

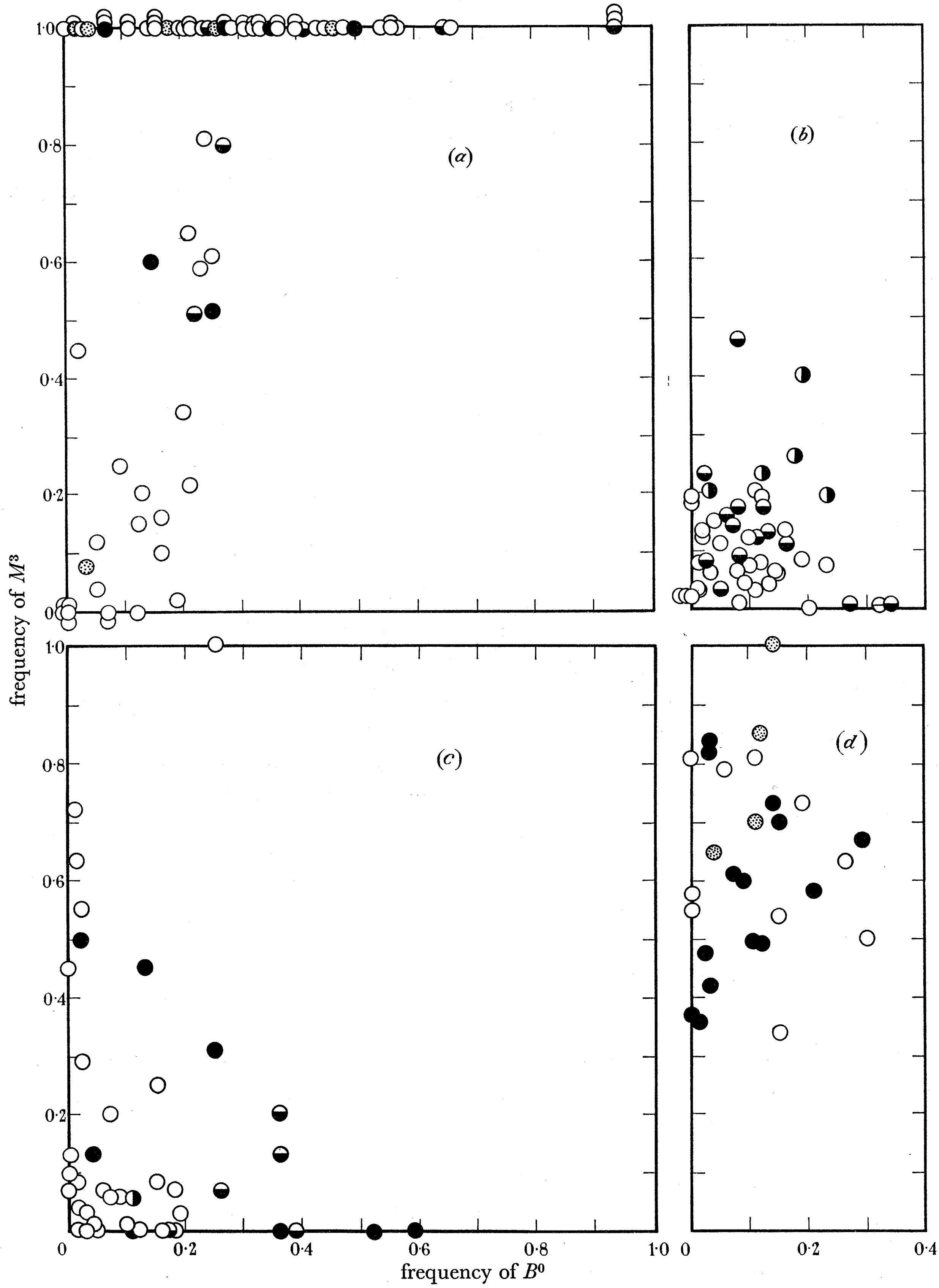

FIGURE 17. Gene frequencies of M^3 and B^0 in *C. nemoralis* (excluding brown shells). (*a*) Marlborough Downs; (*b*) Oxford district (large samples and extreme samples only); (*c*) localities on the Chalk other than the Marlborough and Lambourn Downs; (*d*) Lambourn Downs. Only woodland localities symbolized for habitat; rest, plain circles. All samples shown are of more than twenty-one non-brown shells.

there is no choice of phenotype in this respect, there is no need to think that selection is acting to eliminate five-bandeds. But even if five-bandeds were wholly absent, the total population of this area must be so large that mutations from M^3 to M^- must have occurred many times, and provided the necessary material; and moreover five-bandeds do occur, although extremely rarely, and there must be some individuals heterozygous for the non-suppressing gene, M^-.

In figure 17*a*, for the Marlborough Downs, the outstanding feature is the large number of populations with M^3 at 1·0, and the considerable variation in these populations of the frequency of B^0. The small number clustered at $M^3 = 0$ are those at Burderop Down, Coombe Down and nearby, and those with intermediate values for M^3 are geographically intermediate between the non-five-banded and the five-banded areas. The geographical position is well reflected in the frequency of M^3 for each. Such a distribution of frequencies could be caused in one of the following ways. (*a*) The heterozygotes (M^3M^-) are at a disadvantage to both homozygotes physiologically and consequently M^3 has risen to 100% in one area, and sunk to 0% in the other, perhaps fortuitously, the colonies with intermediate frequencies being maintained in this condition by gene-flow. (*b*) Alternatively, selection is acting for one homozygote in one area, and against it in the other, and colonies with intermediate values are either stable because they are in an area with an intermediate selective action and with heterozygotes at an advantage, or are unstable but in an area where the boundary between selection for and selection against each homozygote is continually fluctuating, so that heterozygotes can persist in appreciable frequencies for long periods. We have no information on previous values for frequencies in the intermediate colonies, and so cannot decide between these alternatives on direct evidence.

If there is a general disadvantage of the heterozygote, M^3M^-, the same tendency to fixation or total loss should be seen in other areas. Figure 17*b* is the diagram for colonies in the Oxford district from which there are samples with a total of pinks and yellows more than 75, plus a few smaller samples representing the extremes of known variation. It shows a very different distribution from figure 17*a*. Both genes tend to be low in frequency; when proportions of the effectively unbanded phenotypes are high, this is attained almost indifferently by high frequencies of either M^3 or B^0, or there may be a slight tendency for M^3 to attain higher frequencies. It was shown by Cain & Sheppard (1954) that the proportion of all effectively unbanded shells (00000, 00300, and a few uncommon types) is related to the nature of the background in different types of habitat in this district, and that this relation is due to visual selection. What emerges from figure 17*b*, therefore, is the remarkable fact that the appropriate frequency of effectively unbanded shells can be made up from any relative proportion of 00000 and 00300. Cain & Sheppard have produced evidence that 00000 and 00300 have very similar visual selection coefficients (which is perhaps rather surprising); this diagram supports their contention. There is no trace here of any tendency for M^3 to be at either 100 or 0% of the frequency of effectively unbanded genes, and we can conclude with certainty that there is no *overall* disadvantage of the heterozygote (M^3M^-), although of course this may be so on higher downland if conditions are more stringent there. Since there is no reason to believe that the gene-frequencies in the colonies investigated are not at equilibrium, it is most likely by far that there is heterosis maintaining M^3 in the population and some selective pressure, not visual and varying from locality to locality, which is determining how the effectively unbanded class will be made up genetically in each colony.

As might be hoped, figure 17*c* shows that the frequencies for M^3 and B^0 in colonies on the chalk show a pattern of distribution intermediate between those in figure 17*a* and *b*. In dense beechwoods, a high percentage of five-bandeds is not found, and this would agree with the nature of the background they provide (Cain & Sheppard 1950). The frequency of B^0 does not rise above 0·6; only two colonies have more than 0·4 and the average is at about 0·3; M^3 ranges from 0·0 to 0·5. In open downland localities, a number of colonies have a high proportion of the five-banded phenotype, and the frequencies of M^3 and B^0 are necessarily low in them; but in many, the effectively unbanded phenotype is high, and in these it is principally M^3 that reaches high values; B^0 does not rise above 0·25. These distributions of frequencies suggest strongly that high chalk country is such that locally in it conditions can favour a remarkably high proportion of M^3 and that the Marlborough Downs are probably an extreme example of this general trend. The very high frequency of samples with M^3 at 1·0 on the Marlborough Downs as compared with those from other chalk localities (figure 17*c*) may well be due to the intensity of study given to the Marlborough area. One locality (Dogtail Down), with M^3 at 1·0 is already known outside the Marlborough district and more intensive search in other chalk districts might well produce a distribution more similar to that in figure 17*a*. Our other area of intensive search is on the Lambourn Downs, and figure 17*d* gives its gene frequency scatter diagram. The pattern is intermediate between that of our other chalk localities (figure 17*c*) and that for the non-five-banded area *A* on the Marlborough Downs (figure 17*a*, top). Again B^0 is never high, but M^3 ranges from 0·3 to 1·0 although reaching fixation only once. This pattern confirms that in figures 17*b* and *c*, in suggesting that there is no widespread heterozygote disadvantage at *M*.

Of the twenty-one open downland localities outside the Marlborough and Lambourn districts ten have frequencies of both M^3 and B^0 no greater than 0·1, and a correspondingly low frequency of effectively unbandeds. Open downland colonies, therefore, unlike beechwood ones, are often heavily banded, and those which are, are widely distributed over the chalk country we have visited (table 4). We have thrush-predated material from several of the heavily banded colonies, and heavy banding would be expected as a result of visual selection on open downland (as would a lack of it in dense beechwoods). However, at Chirton Down 1 and 2 and Water Dean Bottom at least, visual predation was certainly acting extensively, and these examples show that in at least some of the open downland areas, with few five-bandeds, the effect of visual predation is being overridden by influences favouring M^3. It is not the case, therefore, that the colonies in figure 17*c* with low frequencies of 00300 and 00000 are those in which visual predation is active and the rest are free from it.

It would seem, then, that the most likely explanation for the situation described from the downs is that there is selection acting especially in certain downland areas to favour 00300 irrespective of what visual predation may be going on in these areas. Since on the Marlborough Downs there is this favouring of M^3 in one area, but in another very similar one M^3 is usually absent, it is possible that under extreme conditions, either the heterozygotes are at a disadvantage, or there are co-adaptations in the genotypes producing alternative optima with M^3 at 1·0 or 0·0.

A further point which emerges from figure 17*a* is that when the frequency of M^3 is at 1·0, the frequency of B^0 may reach a far higher level than with other frequencies of M^3. We do not have a sufficient number of colonies with M^3 at 1·0 outside the Marlborough district to test whether this is a general effect. If it is general, it would seem to indicate that there is some interaction between the loci, either physiological or, less probably, by M^3 in high frequency converting a whole population to effectively unbanded, so that visual selection does not discriminate against (or for) the unbanded gene and it finds its physiologically appropriate frequency.

IX. Colonies with little variation

At two localities on the Marlborough Downs, Sharpridge 2 and Dean Windbreak 2, the variation within the sample is remarkably small, even when the saturation with M^3 is disregarded. At Sharpridge 2 there appear (with a single exception) to be only two types of the chromosome carrying shell colour and banding, namely, pink unbanded and yellow five-banded. All the pinks appear to be dark pinks and all the yellows dark yellows. The exception is one small juvenile pink 00300 which was seen in the colony on 27 June 1959 and could well have resulted from a cross-over. No individual of this class has been seen since during repeated sampling in 1960 and 1961. Nowhere else, either on the Chalk or away from it have we or Cain & Sheppard (1954) found a colony comparable in its restricted variation, since here both yellow unbandeds and pink bandeds (with this sole exception which may be a recent product within the colony) are absent. Only Sharpridge 3 approaches it in peculiarity. So little variation as this within a population could be caused either by very stringent selection, or by the population originating from one or a very few fertilized individuals (the founder effect) or by sampling drift.

If the two colonies with restricted variation were situated among others with the usual high variability of *Cepaea* populations, it would be reasonable to consider that their peculiarities were produced either by the paucity of individuals founding them or by sampling drift. However, the actual situation is not as simple as this, since the numbers of types of chromosome are not high in the neighbouring colonies and some restrictions at least (absence of M^- and G^B) are acting over large areas and probably caused by heavy selection. The Dean Windbreak 2 colony agrees well with those nearby in excess of yellows and excess of mid-bandeds, and differs from them only in taking these excesses even further.

The Sharpridge 2 colony seems to be in contrast to all the others (except that Sharpridge 3 approaches it); the uniqueness is caused, however, by the absence of pink mid-bandeds (which this colony shares with neighbouring ones) in combination with an absence of yellow unbandeds—but a severe reduction in the number of yellow unbandeds is also found in the Preshute Down, Dean Windbreak, Middle Track, upper Dean Bottom, Rockley Down 3, and Shoulder of Mutton 2 and 3 localities, all nearby. It becomes very doubtful, therefore, whether the peculiarities of Sharpridge 2 are more than could be explained by the local area effects. The high proportion of pinks might seem to be explicable by some visual selection, since, as mentioned above, there are drifts of beech leaves at this locality, blown from the nearby beech-clump; but we have never seen any sign of predation of any sort at this colony or at the other Sharpridge ones. Moreover, a rather high proportion of pinks is found locally at several places on the high downs, where there may perhaps be some form of selection for pinks.

Even the extreme paucity of chromosome types, therefore, may not be an argument for drift or founder effect, but explicable in terms of selection. We have made an estimate of the numbers of adults in this population by repeated mark-release-recapture during 1959, 1960 and 1961, and find it to be between 100 and 250 adults; since the snails are hermaphrodites this is probably near the effective size N of the population, and is certainly low enough for chance to affect the gene ratios in it. But they could be maintained equally well by selection. While it may be possible, then, that the Sharpridge 2 colony has been affected by chance fluctuations in gene ratios, this cannot be asserted with confidence.

X. ESTIMATES OF NON-VISUAL SELECTION IN *CEPAEA*

It seems highly probable (Cain & Sheppard 1954) that polymorphism in *Cepaea* is normal and stable, i.e. balanced, not transient, and is maintained by selection. Fisher (1930*b*) has shown that a balanced polymorphism will result when the selective advantage of a heterozygote is greater than that of either of the corresponding homozygotes, i.e. when

$$\frac{p}{q} = \frac{b-c}{b-a},$$

where p and q are the frequencies of the two allelomorphs x and y and a, b and c the selective advantages of the genotypes XX, XY and YY, respectively. From this expression it follows that

$$q = \frac{b-a}{2b-a-c}.$$

Since in many localities, visual selection is operating to upset the balance of the polymorphism in *Cepaea*, there must be some opposing selective force to maintain its stability, and heterozygote advantage seems much the likeliest.

Among the colour morphs of *Cepaea nemoralis*, dominance is not always complete (Cain *et al.* 1960) but the incompleteness is slight and not likely to be noticed by a visual predator. Let the selective advantages just given be due to non-visual selection. In addition, there is visual discrimination, C, between the recessive homozygote and the other two genotypes. The selective advantage of the recessive homozygote will then be Cc. If we further assume as a simple hypothesis that the heterozygote advantage does not vary greatly from one locality to another, we can write $b = 1$, and the frequency of the recessive allelomorph at equilibrium will be given by

$$q_e = \frac{1-a}{2-a-Cc}.$$

Then visual selection can destroy the balance of the polymorphism when

$$Cc \geqslant 1, \quad \text{since} \quad a < 1.$$

We are also assuming no violent interaction between the various allelomorphs which in fact make up the polymorphism, at least at the shell colour locus, so that we can take all the yellows as one fictitious allelomorph and the various pinks and browns together as the other. There is in fact no strong negative correlation between the colour classes. Moreover, in some colonies containing browns, pinks and yellows, including Rockley North, Rockley 4 and Rough Down, it is possible to determine the proportions of brown/pink to brown/yellow heterozygotes, and these agree astonishingly well with the proportions calculated from the observed frequencies of pinks and yellows using the Hardy–Weinberg equation (Cain *et al.* 1960). It seems best to assume, then, that there is no violent interaction between the colour morphs, at least. Wallace (1958) points out the danger of arguing from agreements of observed and expected frequencies calculated from the Hardy–Weinberg formula; but he is referring to populations not in genetic equilibrium.

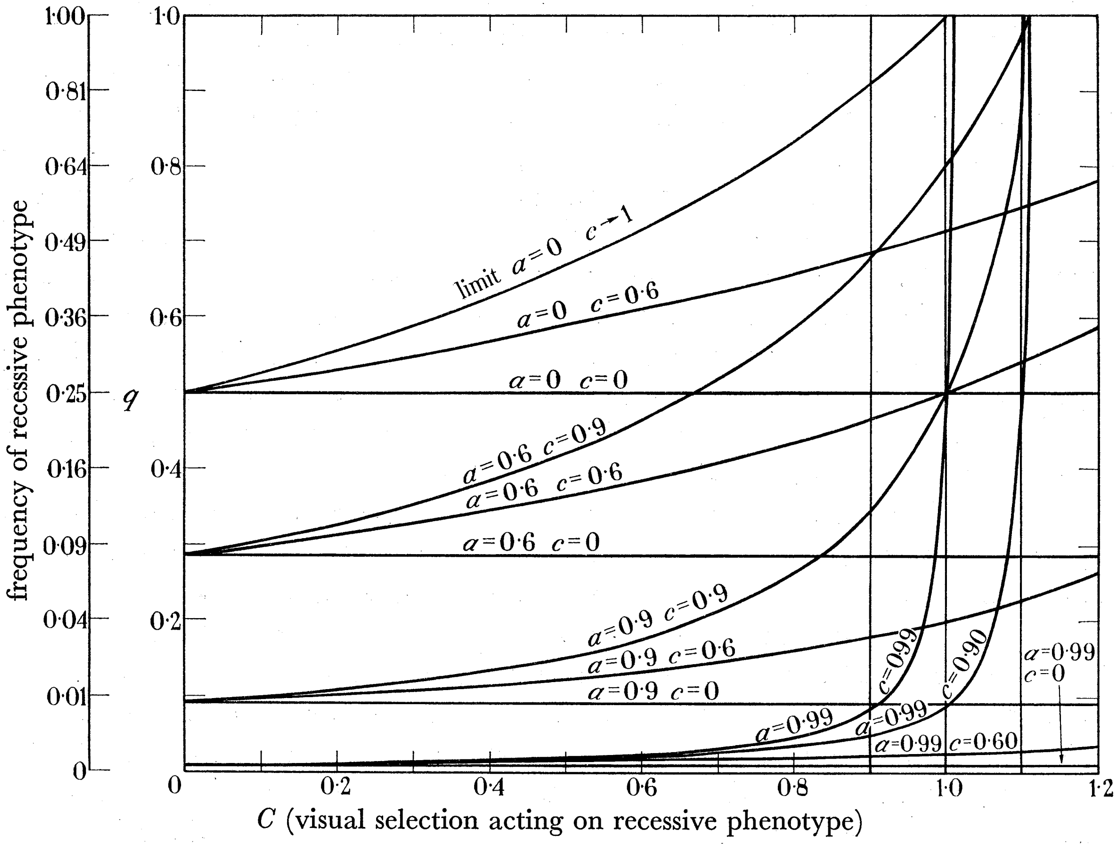

FIGURE 18. Families of curves relating q, frequency of a recessive allelomorph in a polymorphism stabilized by heterosis, to visual selection on the homozygous recessive (C), and physiological selection on this (c) and the dominant homozygote (a).

Some families of curves relating q, a, c, and C are given in figure 18. It will be seen that even for a large change in C from 0·9 to 1·1 (i.e. from 10% selection against yellows to 10% selection for them) a large range of values of q are obtained only if the values of a and c are both between about 0·9 and 1·0, that is, if the heterozygote advantages over the homozygotes ($1-a$ and $1-c$) are rather small. In *C. nemoralis* Sheppard (1951*a*) has demonstrated quantitatively differential predation on different colours, and Cain & Sheppard (1954) have done the same for banding. Sheppard's data suggest a minimum of 1% selection in favour of yellow shells on backgrounds as green as those in a mixed deciduous wood in late spring, or against them on backgrounds as brown as the same one in early spring. On more constant backgrounds such as in dense beechwoods or on open downland, selection may reach to even 5 % or more per year for colour. Of course, we do not know that selection for a colour is at the same strength on one extreme type of background as selection against it on another. Now it is obvious that if visual selection is not stronger than this ($C = 0{\cdot}95$ and $1{\cdot}05$) and yet we find in comparatively undisturbed localities colonies matching their backgrounds well and having some very low and others very high values of q, then a and c can hardly be less than 0·95. Figures 7 and 8 show that these considerations apply to yellow as against other colours in areas away from the downs.

Sheppard's data on selection acting on shell colour in *C. nemoralis* suggest that if thrushes predate these shells visually mainly during the birds' breeding season, when a large supply of food for the growing young is necessary, then since in this period the background in a mixed deciduous wood changes colour the *net* visual selection through the year in this type of habitat may be very nearly nil, and it is noticeable in figure 7 that the phenotype frequencies for yellows observed in mixed deciduous woods (excepting Great Copse, Chislehampton, which has a grassy floor) do cluster about the line for 25 % yellows, i.e. a value of q of 0·5, which again suggests that the values of a and c in *C. nemoralis* are about equal. The woodland samples in figure 16 also tend to support this. Most mixed deciduous woods have a greener background at ground level in summer, but the samples tend to resemble the spring backgrounds more. This suggests that the common thrush and perhaps other birds breeding at about the same time are the most important visual predators, and that visual predation, as contrasted with non-visual predation that thrushes, for example, exert in winter, occurs mainly in spring and early summer, except in unusually dry years when snails might be used longer as food.

At Shoulder of Mutton, we appear to have visual selection effective on colour (p. 25 above), as in areas not on the Downs. Brown is nearly absent from this locality and nearby; in Shoulder of Mutton Wood, $q = 0{\cdot}49$, just outside the wood at Shoulder of Mutton 2 it is 0·80, and at Shoulder of Mutton 4 it is 0·71. If we assume visual selection of $C = 0{\cdot}95$ and 1·05 in the wood and on the downland, respectively, these values suggest that in this area, a for pink only is approximately 0·87 and c is 0·91. If the values for visual selection are 0·99 and 1·01, then those for a and c are 0·97 and 0·98, respectively. Visual selection for colour is also effective at Rockley. At Rockley 2, $q = 0{\cdot}49$, at Rockley 5 and 7 (both downland) $q = 0{\cdot}72$ and 0·68. These figures are remarkably similar to those for the corresponding habitats at Shoulder of Mutton, and suggest similar values for a and c. At Rockley, however, a refers to both pinks and browns, not almost entirely to pinks as at Shoulder of Mutton.

The area effects on the Marlborough Downs produce in some places a great excess of browns, in others of yellows, and in a few places of pinks. In the area of excess browns q ranges from about 0·15 to 0·68, but the lowest values are on open downland where visual selection should be for yellows, as it does seem to be at Fyfield Down 2. If this selection is of the order of 1 %, then taking a as 0·99 (since non-yellows are clearly favoured) c will be 0·934. If a is as high as 0·999, c will be 0·984. Even with very high values of a, therefore, the relative disadvantage of the yellows $(1-c)$ is between 1·5 and 6·6 times that of the non-yellows $(1-a)$. In these areas we have no estimate of the strength of heterosis, which may be greater than in the Oxford area, and the physiological selection against the rarer homozygotes may be very great.

On the Lambourn Downs, in localities where visual selection on colour seems to be effective (Dewdrop Covert 2, Long Covert 1 and 2 and Old Warren 1 compared with Seven Barrows 1, 2 and 3; Sparsholt Firs 1 and 2 compared with Pigtrough Roadside 1 and 2) we get values of q in beechwoods varying from 0·45 to 0·64 and on green habitats from 0·76 to 0·94. These suggest values of a of about 0·97 and of c about 0·985 with $C = 0{\cdot}99$ and 1·01, not unlike those on the Marlborough Downs. In the area of excess yellows there is only one apparently monomorphic colony (Lambourn Roadside); the rest have values of q ranging from 0·81 to 0·99. As explained above (p. 34) we are not certain of where some of the shells in the smallest clumps are being captured by thrushes, but many in the larger coverts are most likely resident. If there is visual selection against yellows in the coverts, and yet q has a value of from 0·81 to 0·92 in them, then on downland, where visual selection is for yellows, the heterozygote advantage will be lost, and one would expect only yellows to occur there; it would seem that here at least visual selection is comparatively ineffective and we have a polymorphism maintained by physiological selection in which the value for a is low in all habitats compared with c, the reverse of the situation in the brown area at Marlborough.

In *C. hortensis*, as is well shown by the data published by Clarke (1960), the frequency of yellow is far greater than that of the other colours, and often no colour polymorphism occurs. When it does occur, yellows still usually make up more than 40 % of the colony, for which phenotype frequency $q = 0{\cdot}63$. This general preponderance of yellows in *C. hortensis* suggests that c is correspondingly greater than a, as compared with *C. nemoralis*. Variation in the appearance of the shell in *C. hortensis* is due more to banding than to shell colour, and Clarke's figure 3 shows that beechwood populations (for example) actually tend to have more yellows than grassland populations—but with more banding and fusion. Because of the masking effect of the bands, therefore, visual selection on shell colour may be far less in *C. hortensis* than in *C. nemoralis*. If we take it as approximately nil ($C = 1{\cdot}0$), then since in Clarke's colonies the percentage of yellow shells is not below 40, for which $q = 0{\cdot}63$, the value of a if $c = 0{\cdot}95$ is 0·907; and if $c = 0{\cdot}99$, a more likely value, $a = 0{\cdot}982$. For the many non-polymorphic and wholly yellow colonies, of course, whatever the value of a, c must be equal to or greater than the selective value of the heterozygotes.

Figure 18 can be used for investigating the effects of selection on banding if q is taken as the frequency of B^B (versus B^0) or of M^- versus M^3 as the case may be, c as the physiological selective advantage for the recessive homozygote, and C as its visual selective advantage.

It can be seen from figure 17 *b* that off the Chalk neither M^3 nor B^0 rises much above 0·45 even in the habitat class, oakwoods, where they can be expected to be favoured visually; on stripy backgrounds both are usually present, but at a frequency of usually less than 0·2 and sometimes much less. This suggests immediately that off the Chalk B^B and M^- have a noticeable physiological selective advantage over their allelomorphs. Both have a mean frequency of about 0·90 when selected for visually and about 0·75 when selected against. If we again assume visual selection of about 1 % (i.e. $C = 0{\cdot}99$ and 1·01), then these frequencies suggest that a is approximately 0·91 and c is 0·98. On downland (figure 17 *a*, *c* and *d*) there is no evidence that B^0 has a greater physiological advantage than elsewhere, except in the non-five-banded area A on the Marlborough Downs, where it appears to increase locally to very high frequencies. The modifier M^3, however, ranges widely over the possible values with no regard for habitat, and *a* presumably varies correspondingly.

It would appear, then, that away from the chalk downs and on them where visual selection is effective, the physiological selection coefficients of yellow and non-yellow homozygotes differ only slightly from each other, and almost certainly do not differ from that of the heterozygote by more than 5%. Unbanded and mid-banded homozygotes, however, seem to be at a greater disadvantage to their heterozygotes and to the unmodified five-banded homozygote. On the downs M^3 reaches very high frequencies but B^0 does not except in the non-five-banded area on the Marlborough Downs. Strong area effects can be produced by alteration of only a few per cent in the physiological selection coefficients, as can the marked phenotype frequency differences between *C. nemoralis* and *C. hortensis*. We have assumed only low values for visual selection; if greater ones are operating, then much larger homozygote disadvantages must be acting to produce the effects observed, as can be seen from table 5.

XI. Body colour

In the preceding sections of this paper, area effects have been demonstrated in polymorphic characters of *C. nemoralis*. This snail shows considerable variation in body colour, which is multifactorially controlled, and not polymorphic. Cain & Sheppard (1952) demonstrated a correlation between the intensity of pigmentation of the protrusible parts of the body, and the percentage of yellow shells in the colony. This they ascribed to the effects of natural selection by predators, the percentage of yellows being a measure of the lightness of the general background, and the body colour being selected, in the same way as shell colour and banding, to be inconspicuous on a particular background. It is now necessary to re-examine their findings, to see if any area effects can have contributed to the correlations they observed.

In figure 19*a* are shown the values for percentage yellows and mean body shade for the colonies reported by Cain & Sheppard, except for two, geographically isolated from the rest (Stretham near Ely; Ashbury, Berkshire Downs). Those shown are all either from the Rockley–Rough Down area, or from the Oxford district. In the figure there is an apparent correlation between habitat (as estimated by the percentage of yellow shells) and the mean body shade within the Rockley–Rough Down colonies, and the Oxford colonies continue this correlation for higher values of mean body shade; but when the Oxford colonies are considered by themselves, no correlation is evident. Cain & Sheppard suggested that the Marley Wood sample (the mixed deciduous wood sample in the figure) combines a high value of mean body shade with a low percentage of yellows because it is from mixed deciduous woodland, which has a background of *light* brown litter. Consequently colonies from this habitat should have light bodies and many pale pink shells, and the correspondence between lightness of background and percentage of yellow shells breaks down for this habitat class. Since really dark backgrounds such as occur in dense beechwoods are not found in the Oxford district it may not be possible from their evidence to distinguish between general lightness of body-shade in the Oxford district because of an area effect, and a lightness due to general lightness of the backgrounds in that district. Consequently the evidence available from the Oxford district is equivocal.

To compare our data with Cain & Sheppard's, it is necessary to use the same method of display as they did but in addition to symbolize by habitat, in order to recognize those colonies that are expected to have light bodies but few yellows (like Marley Wood). In

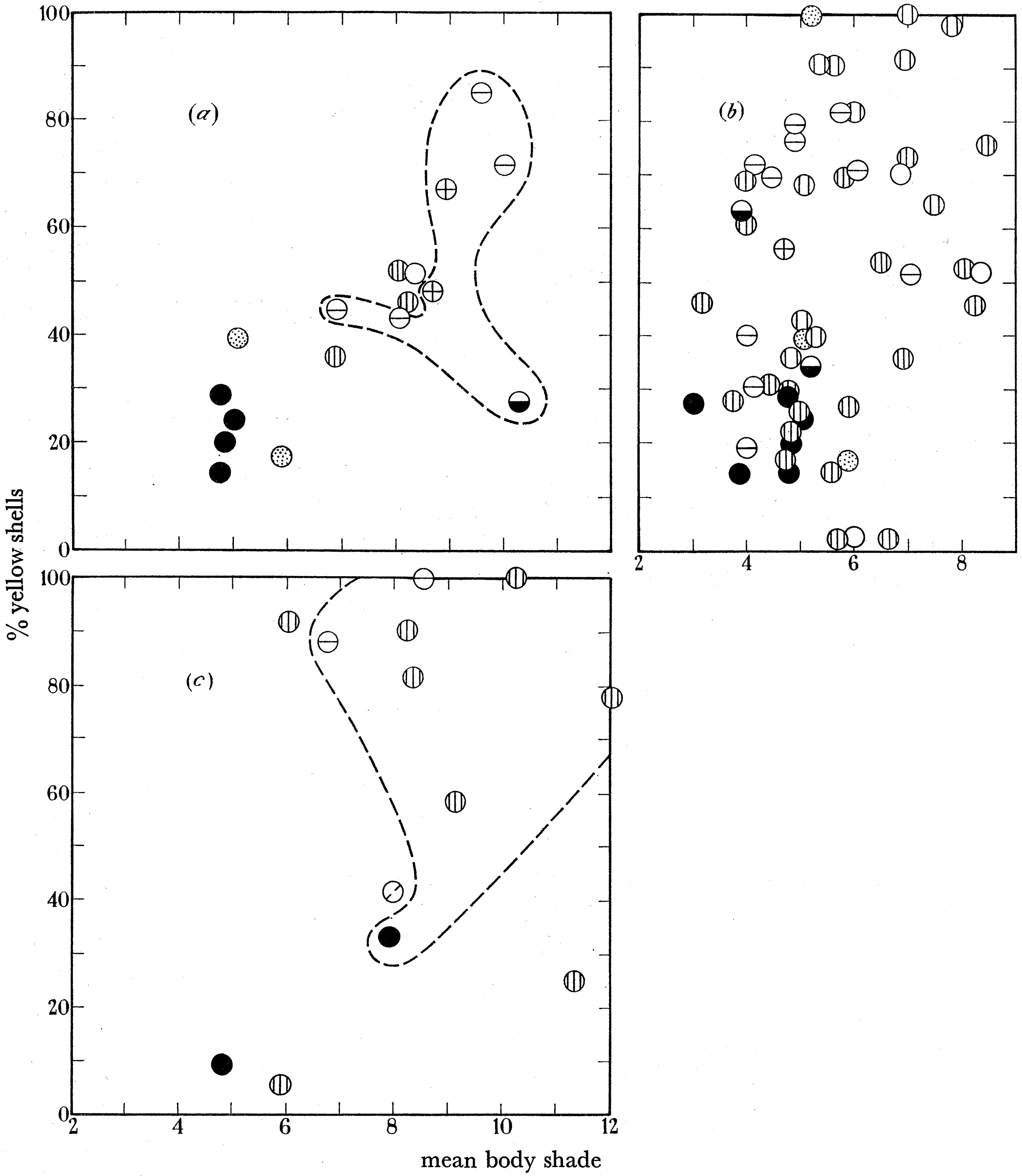

Figure 19. Scatter diagram for percentage yellow shells, mean body shade, and habitat in *C. nemoralis*. (*a*) the Rockley and Rough Down samples, and colonies near Oxford (within line) as reported by Cain & Sheppard (1952). (*b*) All samples from the Marlborough Downs scored for body shade (including Rockley and Rough Down). (*c*) Lambourn Downs (within line) and elsewhere.

figure 19*b* are the mean body shade, percentage yellow shells, and habitat for all but our very smallest samples of live snails from the Marlborough Downs.

At Rockley, from Cain & Sheppard's data, there is an apparent regression of mean body shade on habitat as estimated by eye or by percentage yellows; the regression is in the direction expected if visual selection is effective there, and it is known both that thrushes are active in this area and that shell-colour also corresponds with background in it. In figure 19*b* there is a regression of mean body shade on percentage yellows, but with a far steeper slope than that seen in Rockley 1 to 9. Unfortunately there are very few woods, and of these, two, Rockley North 1 (mixed deciduous, 34·1% yellows, 5·2 mean body shade) and 3 (beech, 27·1% yellows, 3·0 mean body shade) are close to Rockley 1 to 9 and may belong with them as far as visual selection on body shade is concerned, nor is there anything to show that Rockley Down 2 (beech, 13·8% yellows, 3·8 mean body shade) does not also belong there. Such as they are, they tend to support the Rockley regression in figure 19*a*. The only other wood (Barbury Road 8 (4I), mixed deciduous) was a small patch of thorns, probably open formerly to much gene-flow from the surrounding downland.

Because of the strong area effects involving shell colour already described, there is very little association within each non-woodland habitat class between percentage yellows and mean body shade; nor is there any definite sign of association between mean body shade and habitat class, although some might be expected, even within this restricted range of habitats. The area of many five-bandeds (*C*) is not characterized by any distinctive distribution of mean body shade. The main area of excess brown shows an apparent reversed association between percentage yellows and mean body shade, and might perhaps require separation from the rest. In the remaining areas, there is no obvious tendency to area effects in mean body shade, and little if any association between mean body shade and habitat class, except that the higher values for mean body shade seem to occur on more or less open downland.

Analysis by Dr M. G. Bulmer of the data shows that there is no significant influence of banding on body colour. Shell colour, however, does have an influence. Taking brown as standard, yellows do not depart from them significantly in body colour, but pinks do, being on the average 0·75 of one unit of body shade darker than yellows and browns; this accounts for rather more than half the regression shown in figure 19*b*. There is also a significant association between body shade and percentage of yellow shells at each locality (0·006 of one unit of body shade per 1% yellows) which accounts for the remainder of the regression.

The significant association between pink shells and darker bodies suggests a pleiotropic action of the shell-colour alleles on body shade, or less probably, linkage between them and genes modifying body shade. That between percentage of yellow shells and body shade, however, suggests that selection must be acting on both characters, as has been pointed out to us by Dr P. M. Sheppard. This regression gives us no indication of the nature of the selective forces of course; but the distribution of habitats in figure 19*b* suggests that it cannot all be due to visual selection.

Colonies from the Lambourn Downs are shown in figure 19*c*. All those shown are from downland grass or rough herbage except Long Covert 3 (33·3% yellow, 7·9 mean body shade) which is from a beechwood. They show a wide range of values of mean body shade, which average much higher than do those in similar habitats from the Marlborough Downs. There appear, therefore, to be distinct area effects in these two districts, with bodies much lighter on the Lambourn Downs than on the Marlborough Downs. Long Covert 3 is darker, however, than nearby grassland colonies (Seven Barrows 2, 58·1% yellows, mean body shade 9·1; Seven Barrows 3, 77·8% yellows, mean body shade 12·0; Lambourn roadside 100% yellows, mean body shade 10·2) but still much lighter than those from the Rockley beechwoods. There may, therefore, be some visual selection on the Lambourn Downs.

Of the remaining localities in figure 19*c*, which are widely scattered geographically, two from downland grass (King's Play Hill, 5·4% yellows, 5·9 mean body shade; Dogtail Down, 25% yellows, 11·3 mean body shade) differ considerably; indeed the value for Dogtail Down is the highest yet recorded except for one from the Lambourn Downs. This confirms the impression got from comparing the Marlborough and Lambourn Downs, that there may be great variation from colony to colony within a habitat class, and probably considerable area effects. The beechwood sample, from Ashbury, does have very dark bodies, and agrees well with the Rockley beechwoods. Only further collecting can determine whether it is in agreement with its habitat or its area.

It appears, therefore, from the comparison of the Marlborough Downs and Lambourn Downs data that there are area effects in body colour, although none was detected within the Marlborough Downs district. Consequently the Oxford data reported by Cain & Sheppard should not be used to support their correlation without further investigation both in that area and (in view of the association between pink shell and body shade) at Rockley.

Lamotte (1959) has suggested that dark shells (pink and banded) are at a disadvantage in open sunny localities, while pale ones (yellow and unbanded) are at an advantage because of the effects of insolation. If the same selection acts on the colour of the body, both of the mantle seen through the shell, and the protrusible parts, then one would expect pale bodies in open habitats and dark ones in shaded places; unfortunately a similar association might be expected on the hypothesis of visual selection, and since both forms of selection may well be acting, it is difficult to decide on their relative importance. But while in a few of our colonies, snails on open grassland are pale-bodied (mean shade greater than 7·5), in most they are not, and this argues against Lamotte's hypothesis.

XII. VARIATION IN *CEPAEA HORTENSIS*

Clarke (1960) has shown that in *C. hortensis*, as in *C. nemoralis* away from the higher downs, there is a correspondence between sample composition and background, but achieved by different means phenotypically and genetically. *C. hortensis* is normally yellow, browns and pinks being uncommon. Where dark unbanded shells would be common in *C. nemoralis*, he finds in *C. hortensis* yellow five-banded shells with the bands fused together, often completely, to give a nearly uniform dark appearance. In consequence, the correspondence with background is demonstrable in *C. hortensis* by plotting a scatter-diagram not of percentage yellows against percentage effectively unbandeds (as in *C. nemoralis*) but of percentage yellow 00000 against percentage shells with fusions in the class of banded shells which can show fusions.

Since we have shown such marked area effects in *C. nemoralis* on the Marlborough Downs, it is important to see what modes of variation *C. hortensis* exhibits there. Figure 20*a* shows all our *C. hortensis* samples of more than twenty snails from that district, plotted

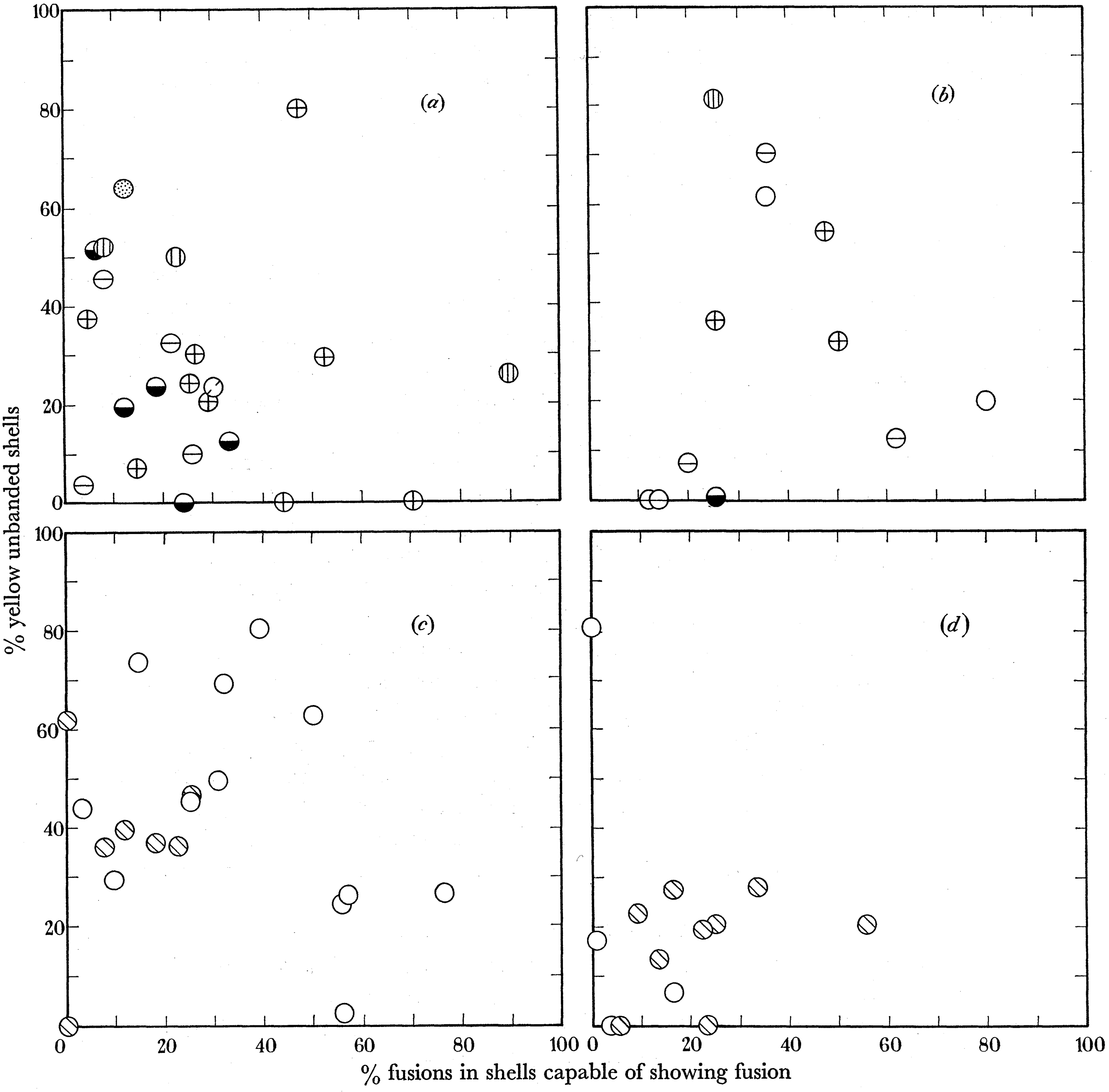

Figure 20. Scatter diagrams for percentage yellow unbanded shells, percentage fusions in shells capable of showing fusions, and habitat in samples of *C. hortensis* of over 20 shells. (*a*) Marlborough Downs; (*b*) samples newly reported for localities other than on the Marlborough Downs; (*c*) samples from grassland both on the chalk (open circles) and elsewhere (circles with diagonal lines) reported by Clarke 1960; (*d*) samples from hedgerows and rough herbage on the Chalk (open circles) and elsewhere (circles with diagonal lines) reported by Clarke (1960).

according to Clarke's system, and figure 20*b* samples not from that district, which are all on chalk except for the Erlestoke sample (from the foot of a chalk scarp). We have included all adult specimens found while Clarke excluded intact dead shells; this difference has no important effect here. Clarke has shown in his figure 4 all the samples of *C. hortensis* available to him; in figures 20*c* and *d* in the present paper are shown, for comparison with figures 20*a* and *b*, his data on grassland colonies and on hedgerow and rough herbage colonies, both on the high downs and in other districts. We have only two grassland samples from the Marlborough Downs (figure 20*a*) about which nothing particular can be said. However, our three grassland samples from chalkland elsewhere (figure 20*b*) agree well with Clarke's chalk grassland samples (figure 20*c*). We have not made a special investigation of *C. hortensis* away from the downs, but comparison of Clarke's colonies on and off the Chalk (figure 20*c*) suggests strongly that there is more variation between chalk grassland colonies than between grassland colonies elsewhere, and therefore that the downs may have diverse area effects both in *C. hortensis* and in *C. nemoralis*. Our woodland samples from the Marlborough Downs shown in figure 20*a* seem to agree well with Clarke's samples (1960, figure 4) except that they all have a low proportion of fusions, and that Wroughton Copse has too many yellow unbandeds for its background. Our samples from rough herbage and hedgerows on chalkland other than the Marlborough Downs (figure 20*b*) show a wide scatter, and tend to contrast in this with Clarke's samples from these habitats both on chalkland and elsewhere (figure 20*d*). Our samples from these habitats on the Marlborough Downs (figure 20*a*), a comparatively restricted district, show rather less scatter, and, like the woodland samples from the same district, have rather few fusions. This suggests, therefore, the possibility of an area effect on the Marlborough Downs depressing the proportion of fusions, and (figure 20*b*) a considerable diversity of area effects on chalkland as opposed to elsewhere (figure 20*d*). The suggestion is supported by Clarke's grassland samples (figure 20*c*) which also show great diversity on chalkland; his from elsewhere are much more homogeneous but all are from the Oxford district, so that here too there could be an area effect, but a comparison of them with those from other habitats in the same district (hedgerows and rough herbage, figure 20*d*; woodland, Clarke (1960, figure 4) shows that there are strong consistent differences with habitat. Clarke (1960, p. 439) has pointed out two local occurrences of dark-lipped pink shells and 00300 near Oxford. From his tables these are area effects comparable in magnitude with that involving spread bands in *C. nemoralis* reported above (p. 14).

It appears, then, that although visual selection is important in *C. hortensis*, there is evidence for area effects on the Chalk in this species also, but they do not seem on the evidence available to produce complete fixation of any particular gene. Yellow is so commonly the only colour in *C. hortensis*, that its fixation can hardly be described as an area effect.

XIII. DISCUSSION

Before discussing the relative importance of 'genetic drift' and selection in *Cepaea* it is necessary to be quite sure of what is included in the concept of 'genetic drift', since its principal exponent, Sewall Wright, has recently complained (1956) of much misunderstanding. A very common impression is exemplified in Falconer's important survey of quantitative genetics (Falconer 1960, p. 53) where he states with reference to Buri's work

(Buri 1956) that 'These changes of gene frequency resulting from sampling in small populations are known as *random drift* (Wright 1931)'.

A careful re-reading of Wright's (1931) paper seems to strengthen this impression. For example, Wright says of individual genes in small populations (1931, page 147) 'They drift from one state of fixation to another in time regardless of selection...', and the word drift seems admirably chosen to label the aimless fluctuations resulting from random sampling errors, as opposed to the effects of selection. In this paper Wright was concerned to find expressions for distributions of gene frequencies that would include the effects of population size, migration, mutation and selection. He concluded that in large populations with strong selection acting there would be almost complete fixation of the favoured gene for each locus (1931, p. 149). 'Here also there is little possibility of evolution. There would be complete equilibrium under uniform conditions if the number of allelomorphs at each locus were limited. With an unlimited chain of possible gene transformations, new favourable mutations should arise from time to time and gradually displace the hitherto more favoured genes, but with the most extreme slowness even in terms of geologic time.'

Wright's attitude to selection at this time is understandable in view of the very few indications then available of the size of selection-coefficients to be found in the wild for even 'trivial' characters, and the unfortunate tendency of some taxonomists to assert (on no good basis) that interspecific and intergeneric characters at least were non-adaptive (Wright 1932, pp. 363 to 364). It is not surprising, therefore, that people reading this paper have taken genetic drift to refer to the cumulative effects of random sampling errors. Wright concluded (1931, 1932) that a combination of subdivision of populations, fluctuations due to random causes, and selection, gave the best opportunity for rapid evolution.

Later (1935, pp. 265 to 266) he stressed the importance of small local changes in selection in facilitating the production of new gene combinations, but did not yet describe them as 'random', nor assimilate them directly to random changes due to sampling error. In 1955, he re-classified the modes of immediate change of gene frequency into:

(1) Directed processes (the resultant changes being determinate at least in principle): recurrent mutation, recurrent immigration and cross-breeding, and mass selection.

(2) Random processes (the variances of the resultant changes being determinate at least in principle): fluctuations in mutation rate, fluctuations in immigration effect, fluctuations in selection, and accidents of sampling.

(3) Unique events, not amenable to statistical treatment. Consequently he was consistent in saying later (1959, p. 86) that 'the founder principle in its random aspect is merely one form of random drift....'

Previously (1955, p. 18) Wright had used the word drift in connexion with the effects of selection, mutation, migration, etc., as follows. 'The directed processes may be described as producing a cumulative *steady* drift in gene frequency, complementing the term *random* drift that has been used for the cumulative effects of the random processes. The common restriction of "random drift" or even "drift" to only one component, the effects of accidents of sampling, tends to lead to confusion.' In the 1931 paper, Wright did not *define* any special use of the word drift, and his use of it in connexion with steady processes seems not to be objectionable; but in fact the term 'genetic drift', referring to the cumulative effect of sampling errors (and sometimes to the effect of these and other random changes) has become a definite technical term (Dobzhansky 1951 and 1959, p. 85; Falconer 1960) and in the present circumstances it is highly desirable to define it or avoid it as causing confusion. Whatever may be the conveniences for mathematical geneticists of considering together all processes regarded as random, irrespective of their biological significance, the worker on actual examples must classify processes according to their biological significance; and Wright admits himself (1955, p. 18) that there is no good distinction between a secular change in a coefficient describing a directed process and a fluctuation. 'As with the unique processes, it is a question of the span of history that is in mind.'

Not only is there no good distinction in theory between fluctuations and long-term changes, but in practice the lumping of 'random' processes prevents the proper analysis of actual situations. The field worker becomes liable to confuse under one name, for example a great diversity of gene-frequencies in small populations caused primarily by sampling error in the absence of strong selection and local diversity of conditions on the one hand, and, on the other, a similar diversity caused by corresponding diversity of local selective forces but at present not in equilibrium because of disturbance of the habitats. Such confusions can only lead to erroneous general conclusions about the relative importance of selection, sampling error, mutation and other factors.

Any given selection pressure may well vary from minute to minute, but it is still desirable biologically to recognize it as selection, and to contrast it in some circumstances with the effects of random sampling error. Similarly (Dobzhansky 1959, p. 85) it is desirable to recognize the founder effect as such even if in the eyes of the mathematical geneticist it 'in its random aspect is merely one form of random drift...' (Wright 1959, p. 86). Sampling error is biologically a very different phenomenon from selection, and as Wright has declared that 'genetic drift' must have a wider connotation, we propose to refer to the effects of sampling error as *sampling drift*.

Many authors at different times have stated that much if not all of the interpopulation variation in *Cepaea* is random. This has been asserted for two rather different reasons. On one hand, it has often been said (see Cain & Sheppard 1954 for references) that such trivial characters as different colours or numbers of bands on a shell can have no selective value, and therefore are excellent material for 'genetic drift' to work on. Such statements wholly neglect the likelihood that the *genes* controlling the characters may have considerable selective value; and moreover, as Cain (1951 *a*, *b*) has pointed out, they are not based on any positive information but merely on complete ignorance of the actual significance of the characters. A biologist may be able from his own experience to guess at the significance of some apparently trivial characters in some of the vertebrates most nearly allied to him, but we simply do not know enough of the biology of most organisms to be able to give a useful judgement based merely on the existence of a variation, or on this and its geographical distribution.

On the other hand, Lamotte (1951, 1952), came to the conclusion, as a result of excellent and extensive fieldwork in France, that variation was almost entirely at random, that visual selection could not be of any importance, and that the polymorphism was maintained by a surprisingly high mutation rate. More recently (1959) he has abandoned the hypothesis of exceedingly high mutation rates, and shown experimentally that physiological selection by climatic factors is likely to be of importance, as had been stated already for *C. hortensis* by various authors. His estimate of the effectiveness of 'genetic drift' is reduced by this, but he still considers, from a comparison of variances in groups of large and small colonies, that it has a marked effect. He has now found on re-examining his data (Lamotte 1959) that there are correlations (in Provence and Normandy) between colony composition and background, but his efforts to detect corresponding visual selection by predators have not in general succeeded. Moreover, he has brought forward again an argument based on the variation in mixed populations of *C. nemoralis* and *C. hortensis* showing in his opinion that visual selection is unimportant. He concludes therefore that climatic selection and 'genetic drift' are the principal factors, besides disturbance of habitats by human or other action, that determine intercolony variation. The comparison that Lamotte makes between variances in large and small colonies is carried out absolutely irrespective of the circumstances of these colonies. He says himself (1959, p. 82) that 'the large populations are more often found in well-defined biotopes, such as woods or large meadows. The small colonies are more often in intermediate environments such as hedges and gardens.' But hedges and gardens are more likely to be disturbed than large woods or meadows, and it is quite possible that what Lamotte has shown is merely that in disturbed habitats populations tend to be small, and not at all that smallness of the populations is the factor allowing random effects to produce greater variance. A mere comparison of the genetic variance of populations of different sizes irrespective of their circumstances is valueless for determining the relative roles of sampling drift and selection of any type. With respect to visual selection, this had been already pointed out by Cain & Sheppard (1954).

The difficulties attending the direct detection of visual selection have been discussed by Cain & Sheppard (1961). A failure to detect it may well have no significance. Lamotte's argument from mixed colonies is that thrushes do not distinguish between *C. nemoralis* and *C. hortensis* and that if visual selection is important, there should be a correlation between the frequencies of the same variety in the two species in each mixed colony. He finds only a very slight correlation, and considers that this proves the unimportance of visual selection. But, as Cain & Sheppard (1954) pointed out, such a correlation could be expected only if the physiological selective values of each allelomorph were about the same in both species, and further, if the visual selective value of any one allelomorph is independent of which allelomorphs at other loci it is associated with in each population. They suggested this, having found on the one hand that in colonies of *C. nemoralis* in which visual predation was important, the unpopular colour class pink was significantly more heavily banded than the yellows, and having noted on the other hand (as had many others) the great differences in overall frequency of particular allelomorphs in *C. nemoralis* and *C. hortensis*, which indicates immediately that they are not physiologically equivalent.

Clarke (1960) has made a special study of the question and has shown that thrushes appear to be not only bad taxonomists but bad geneticists as well. Not only do they fail to distinguish selectively between the two species, but it seems that they will treat a brown unbanded *C. nemoralis* as selectively equivalent to a yellow five-banded *C. hortensis* with its bands fused together. Consequently, since browns and pinks are so rare in *C. hortensis* that they must be at a considerable physiological disadvantage in this species (but not in *C. nemoralis*), on the darker and more uniform backgrounds, populations of *C. hortensis* show a large number of yellow five-bandeds with much fusion of the bands, while *C. nemoralis* produces red and brown unbandeds.

The data so far published by Lamotte do not in fact allow us to obtain an estimate of the relative importance of visual selection, physiological selection, sampling drift, and the founder effect in French populations of *C. nemoralis*. It may well be that visual selection is less important, and insolation and disturbance of the habitat much more important in France than in Britain, but this cannot be regarded as established yet. As Lamotte himself has remarked (1959), it is very difficult to determine the roles of systematic and fortuitous agents in affecting gene frequencies in the wild. Even in the laboratory it is difficult to show that conditions in a large number of small populations have been kept effectively the same, and that sampling drift has occurred, although this has been done successfully by Buri (1956). In the wild, where no two colonies are likely to be in exactly the same circumstances, direct proof is usually impossible. Selection can of course be demonstrated if its agent can be seen at work, as when birds are observed to predate non-melanic moths selectively in industrial areas, for example (Kettlewell 1956, 1961). When, as is far more usual, the agent cannot be seen at work, selection can be considered as demonstrated if we find one of the three following situations.

(1) A strong association is observable between the frequency of a given allelomorph in various populations and some variable in the environment (physical or biotic). This does not, of course, demonstrate that the environmental variable is the active selecting agent; it may be only a concomitant.

(2) In a single population over a period of time, a change in gene frequency takes place, which, it can be calculated, is too great or too constant in direction to be attributed to mutation, migration and sampling drift (e.g. Sheppard (1951 *b*) on *Panaxia dominula* at Cothill near Oxford).

(3) Although neither an association with any environmental factor, nor the detailed history of the populations is known, the geographical distribution of the gene frequencies shows that area effects like those described in the present paper exist *and* there is good evidence that they are not produced by spreading from former refuges. The areas must be large compared with the size of a panmictic population, as in the present study.

Even when some selective forces have been demonstrated and their strength determined and effects estimated, it is rash to assume that the residual genetic variation can only be due to random effects. In the wild it is far more likely that all the selective influences have not been identified. We must be guided by the mathematical demonstration (Fisher 1930 *a*) that for sampling drift to have a marked effect all selection on the allelomorphs concerned must be very slight, and the populations involved rather small (see Falconer (1960) for a review).

Certainly 'drift' has often been hastily postulated to explain puzzling distributions of gene frequencies. But when the situation has been thoroughly investigated, its role has been shown to be smaller than was originally claimed or even negligible. This has happened in such diverse characters as chromosome inversions in *Drosophila* (Dobzhansky & Queal 1938; compare Wright & Dobzhansky 1946), flower colour in *Linanthus parryae* (Epling & Dobzhansky 1942; compare Epling, Lewis & Ball 1960); blood groups in man (Wright 1940; Dobzhansky 1951; compare Mourant 1954, the review in Huxley 1955 and Chung, Matsunaga & Morton 1960), and shell colour and banding in *Cepaea* (Diver 1940; Lamotte 1951; compare the present paper, Cain & Sheppard 1954, and Lamotte 1959). To say this is not to deny that random processes may occur in wild populations, but to try to find out what their importance actually is.

It is much to be wished that a good example of sampling drift in wild populations should be identified. This could be done in such an organism as *Cepaea* if the history of several adjacent colonies was followed over a period of years and it could be shown that the gene frequency in one of them, but not the others (which act as the controls), had altered as the result of non-selective events. These could be, for example, repeated local burnings or ploughing-up which are certainly not related to the composition of the colony and are observed to leave each time survivors that form unrepresentative genetic samples of the colony as it was just before each event. If the resulting changes happened to be cumulative there would be no reason for thinking of them as being other than sampling drift.

Cain & Sheppard (1950), in opposition to the then general opinion that variation in *Cepaea* was merely random, demonstrated that visual selection by predators was influencing strongly the proportions of morphs in the populations they investigated. They concluded that the polymorphism is maintained by physiological selection, but the balance so produced is swayed by visual predation; and they suggested that the physiological balance could differ in different districts (Cain & Sheppard 1950, p. 287). Further work (Cain & Sheppard 1952, 1954; Sheppard 1951 *a*, 1952) confirmed the importance of visual selection on both shell characters and body colour, and enabled them to make tentative estimates of its strength in some situations. A few anomalous populations were found which, however, had much in common and were provisionally accounted for by Cain (1953) as affected by tone-predation by mammalian predators.

The present study has confirmed the importance of visual selection in causing inter-population variance in England north of the Chalk from Bristol to Cambridgeshire and as far north as Leicestershire, and in places on the Chalk itself. On the higher downs, however, the area effects we have described show that there are other factors at work that can override the effects of visual selection and act even if the latter is absent. These factors do not include, apparently, the chemical nature of chalk itself, since at several places on the Chalk, including the Wittenham localities (p. 38 above) we have populations showing no indication of an area effect, and considerable hints of the effectiveness of visual selection.

The area effects are far too homogeneous over large areas, containing very large numbers of individuals, to be due to sampling drift or any other random process acting at the present. The non-five-banded area, for example, is approximately a triangle of base 6·5 km (4 miles) and height 5·5 km (3·5 miles) as compared with a panmictic unit of perhaps only 40 m diameter. Moreover, since we have good evidence that visual selection is being exerted at Fyfield Down 2, where snails are abundant and the population size is probably very large, it seems highly unlikely that the conditions necessary for drift to exert a large effect are fulfilled there. For the Marlborough Downs as a district, we have evidence that a former reduction to a few tiny populations that could be subject to sampling drift, and a subsequent expansion are highly unlikely. Indeed, there is evidence (§V, 3) that at least one of the area effects on the Marlborough Downs may have been acting during and since the Neolithic period. And, moreover, those colonies which by their restricted variation suggest most strongly that some random process is acting (§IX) turn out to be only extreme examples of local tendencies.

Consequently, it seems that some systematic processes are at work. We have some clues as to possible selection by climatic factors of at least the brown morphs (§VIII, 3). No indications of actual causes are available for banding, but our study of gene frequencies (§VIII 4) shows that there is a strong tendency for M^3 to reach far greater frequencies on the higher downs than elsewhere. Further intensive studies of areas on and off the Chalk are now required. The higher chalklands seem to be the formation most prone to produce such effects, but no doubt other high calcareous districts will also show them.

The area effects described in this paper are characterized by both an unusually high frequency of one allele at one or a few loci, and a relative constancy of these high frequencies over an area containing very different habitats, in which visual selection is acting, which elsewhere produces local differentiation. It is quite possible that a similar constancy may be found over a large and diverse area but without any one allele predominating. This could happen, for example, if heterosis were very strong (§X), and the result could still be referred to as an area effect.

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APPENDIX

DESCRIPTIONS OF LOCALITIES ON THE MARLBOROUGH DOWNS

(1) *Crooked Hedge*, 2B Hedgerow (green)	Old thorn hedge, one tree thick; much nettle, umbellifers, and grass. Colour near ground rather green for a hedge. Cultivation on both sides
(2) *Pickledean*, 4B Beech (dense)	Dense beechwood with elders and some ivy, large drifts of beech-leaf litter

(3) *Parsons Penning 1*, 3B Short turf	Open downland with sarsens
(4) *Parsons Penning 2*, 3B Short turf	Open downland
(5) *Parsons Penning 3*, 2C Nettles-in-grass	Nettle patch in open downland
(6) *Parsons Penning 4*, 2C Nettles-in-grass	Short and long grass with some nettles and many large sarsens
(7) *Parsons Penning, 5*, 2C Long grass	Long downland grass alongside fence, with a very few nettles
(8) *Parsons Penning 6*, 2C Hedgerow (mixed)	Alongside the Ridgeway, with cultivation behind it and on the other side of the Ridgeway. Very mixed habitat with old thorn trees, elders, nettles and short grass. At north end, grass and nettles with a little gorse and some thorn, many sarsens and old tree-stumps
(9) *Overton Down 1*, 3C Short turf	Short downland turf with much burnet and sorrel dock. Some scattered elders and gorse with a few sarsens, some thistles and nettles; mostly downland
(10) *Overton Down 2*, 3D Long grass	Downland grass with sarsens, a few nettles in places
(11) *Overton Down 3*, 3C Nettles-in-grass	Minute pit with elders, surrounded by downland grass, with nettle clumps near the edge of the pit
(12) *Overton Down 4*, 3C Nettles-in-grass	Small clumps of nettles in open downland in long grass
(13) *Overton Down 5*, 3C Nettles-in-grass	Nettles around sarsens and under a single elder, surrounded by downland grass
(14) *Overton Down 6*, 3D Beech (dense)	A fairly dense beechwood, large areas of red leaf-litter on the ground. Not much undergrowth, a little woody nightshade, and some small elders. Surrounded by open downland
(15) *Overton Down 7*, 3C Short turf	Short downland turf with sarsens
(16) *Clatford Bottom 1*, 4C Mixed deciduous wood	Mixed deciduous copse, partly cut and overgrown with much rough herbage. Surrounded by downland to north and east, by broad path with hedge on south and west
(17) *Clatford Bottom 2*, 4C Long downland grass	Regressing warren on open downland slope. Downland grass and herbs, some nettles and rough herbage
(18) *Clatford Bottom 3*, 4C Long downland grass	Bottom of dry valley in downland; collected around sarsen stones and under one small thornbush. Long grass, a very little rough herbage

(19) *Clatford Bottom 4*, 4C Mixed	Very small thorn and elder copse, dense, with some nettles, surrounded by a narrow belt of bracken and long grass with sarsens
(20) *Clatford Bottom 5*, 4C Mixed	Small clumps of thorn and elder bushes on steep downland slope, surrounded by downland grass
(21) *Clatford Bottom 6*, 4C Beech (open)	End of fir and beech wind-break, with elders, and bare earth beneath them. Abuts on to downland, cultivated fields on either side of wind-break
(21*a*) *Devil's Den*, 5C Long grass	Very long downland grass, with few herbs. Training gallop on one side, cultivated field on the other
(22) *Delling 1*, 3D Mainly long grass	Mainly downland grass with many scattered clumps of thorn and elder, with brambles and bracken at the bases, also a few bramble patches and gorse bushes scattered about, and some sarsens
(23) *Delling 2*, 3C Long grass	Downland grass, rather long, with many sarsens
(24) *Delling 3*, 3D Long grass	Thrush stones under elders, surrounded by downland grass
(25) *Delling 4*, 3C Long grass	Long grass with many sarsens
(26) *Delling 5*, 3C Long grass	As Delling 4
(27) *Wroughton Copse*, 3D Mixed deciduous wood	Mixed deciduous copse, rather dense, with much leaf litter on the ground, and some nettles and rough herbage. Surrounded by a narrow belt of long grass with bracken. Open downland on three sides, heavy grazing on the fourth
(28) *Fyfield Down 1*, 4D Short grass	Disturbed open downland, pits and hummocks with sparse grass
(29) *Fyfield Down 2*, 4D Long grass	Downland grass, rather long, some sarsens, and a few scattered thorn bushes on the balks adjoining
(30) *Fyfield Down 3*, 3D Long grass	Ungrazed stand of very pure grassland
(31) *North Delling 1*, 3D Nettles-in-grass	Cattle-cropped short grass with nettles; a few sarsens and a very few elder trees
(32) *North Delling 2*, 3D Nettles-in-grass	Nettles in short, heavily grazed grass
(33) *North Delling 3*, 3D Mixed deciduous wood	Elders, thorns, beeches, ash, with much bramble and a few sarsens. Much leaf-litter
(34) *North Delling 4*, 3D Nettles-in-grass	Downland grass with very little rough herbage except for several dense patches of nettles; a few sarsens

(35) *North Delling 5*, 3D Nettles-in-grass	Downland grass with many sarsens, and many small clumps of nettles. A very few elders and thorns
(36) *North Delling 6*, 2D Long grass	Alongside the Ridgeway with cultivation surrounding it except that it abuts on open downland to the south-east. Mainly rather long grass, with a line of sarsens (dumped there); very little rough herbage, and only two small bushes (elder)
(37) *Clatford Down 1*, 4D Long grass	Open downland with sarsens and a few clumps of elder and thorn
(38) *Clatford Down 2*, 4D Long grass	As Clatford Down 1, with some clumps of gorse
(39) *Clatford Down 3*, 3D Short grass	Thrush stone under elders surrounded by short poor grass
(40) *Clatford Down 4*, 3D Mixed	Grass with sarsens, some nettles, elders and thorns
(41) *Clatford Down 5*, 4D Long grass	Open downland; grass with many short herbs (burnet, yellow bedstraw, etc.)
(42) *Clatford Down 6*, 4D Mixed deciduous wood (thorn)	Clump of dense thorn trees with almost no vegetation below, some nettles around edge. Surrounded by cultivation and adjoining a strip of rough herbage
(43) *Clatford Down 7*, 4D Rough herbage	Grassy bank with many herbs, and isolated thorns alongside field
(44) *Clatford Down 8*, 4D Rough herbage	Nettle patch at junction of three fences of cultivated fields
(45) *Clatford Down 9*, 4D Long grass	Very long downland grass with sarsens, and isolated thorns and elders
(46) *Totterdown 1*, 4E Nettles-in-grass	Small nettle patch with grazed short turf on one side and long grass at the edge of an arable field on the other
(47) *Totterdown 2*, 3E Long grass	Long ungrazed grass around sarsens in expanse of short grazed grass. A few nettles and thistles
(48) *Totterdown 3*, 3D Mixed deciduous wood	Tangled brake of brambles, elders, ashes and a clump of beech trees, by a ruined cottage
(49) *Totterdown 4*, 3D Mixed deciduous wood	Mixed deciduous wood, surrounded by open downland on three sides, and a pasture on the fourth. Dense woodland (elm, oak, ash, some hazel and elder) with nettles, red campion, twayblade orchids; not much bramble. Considerable leaf-litter
(50)–(58) *Rockley 1–9* *1*, beech (dense), 5D *2*, beech (dense), 5D *3*, beech (open), 5D	Descriptions have been given already by Sheppard (1952). Localities 1, 2, 8 and 9 are beechwood with a carpet of leaf-litter and much open soil; 4, 5 and 7 are open downland; 3 and 6 are prolongations of beech

4, long grass, 5D *5*, long grass, 5D *6*, beech hedge (open wood), 5D *7*, long grass, 5D *8*, beech (dense), 5D *9*, beech (dense), 4D	into downland. The samples used here are those collected by Sheppard in 1951
(59) *Barton 1*, 7C Long grass	Overgrown chalk pit, very small; nettles, thistles and much grass. Surrounded by open downland
(60) *Barton 2*, 6C Open wood	Exactly as Barton 3, about 300 m away
(61) *Barton 3*, 6D Open wood	Downland thickly scattered with bushes and trees congregating in places to woodland, and intersected by gallops. The collection was made from a thrush stone at the edge of woodland near a gallop
(62) *Barton 4*, 6D Rough herbage	Wide grass path, with long grass, thistles, a few nettles and one thorn bush. Cultivation on both sides
(63) *Barton 5*, 6D Mixed	About 100 m from Barton 4, large thorn tree, bare ground beneath, surrounded by bracken grading off into long grass. Cultivation on both sides
(64) *Barton 6*, 6D Mixed deciduous wood (dense)	Small mixed deciduous copse, dense with much bare ground and a few nettles, grading off into open downland; cultivation on other side of path
(65) *Barton 7*, 6D Mixed deciduous wood (dense)	Very mixed deciduous wood with many elders; much rough herbage, and expanses of bare ground. Surrounded on three sides by gallops, on the fourth by more mixed deciduous woodland
(66) *Barton 8*, 6D Mixed deciduous wood (dense)	Mixed deciduous wood, rather dense. Much leaf-litter on ground, few herbs. Some elders and thorns at the edge. Cultivation on one side, open downland and gallops around the rest
(67) *Barton 9*, 6D Mixed deciduous wood	Mixed deciduous wood, dense, with hazel, ash, oak, elders. Much bramble and some green herbage, with large expanses of leaf litter
(68) *Rough Down*, 8C Short grass	Steep downland with short grazed turf
(69) *Temple 1*, 3E Rough herbage	Extensive nettle patch with some scattered elders. Some domestic refuse
(70) *Temple 2*, 3E Rough herbage	Very long grass and nettles beside an open thorn hedge, alongside track; cultivation on one side, sheep pasture on the other
(71) *Temple 3*, 3E Rough herbage	Bank between two arable fields, with some sarsens; long grass, nettles, umbellifers and other herbs

(72) *Temple 4*, 4E Mixed deciduous wood (open)	Open deciduous wood on steep slope. Ash, elder, some beech. Much grass and nettle, very green, very open at ground level. Adjoining farm road, otherwise, surrounded by cultivation
(73) *Temple 5*, 4E Rough herbage (formerly mixed deciduous woodland until at least 1947)	Very rough herbage recently cut back and planted with conifer and sycamore saplings. Line of old thorn, elder and ash trees along edge
(74) *Temple 6*, 5E Hedgerow	Steep grass bank with uncut hedge of hawthorn, some ash, some elder, along top. Rough grass, much nettle and umbellifers, very steep. Road above hedge; cultivation on both sides
(75) *Monkton Down 1*, 2E Nettles-in-grass	Nettle patches in open downland, close to a hedge, beyond which is cultivation
(76) *Monkton Down 3*, 1E Nettles-in-grass	Old shallow chalk pit, surrounded by open downland. Completely grass-grown, with several nettle patches
(77) *Monkton Down 5*, 1E Mixed	Large old chalk pits in side of steep down. Mostly grass-grown with a few scattered thorn bushes, but at the mouth a tiny copse of elder, thorn and brambles
(78) *Monkton Down 6*, 2F Hedgerow	Alongside the Ridgeway, surrounded by cultivation. Elder, thorn, ash, nettles, mixed rough herbage. In parts, almost a small copse
(79) *Berwick Bassett 1*, 2F Hedgerow	Alongside the Ridgeway. Big hedge, with cultivation on one side, open downland on the other. Thorn and elder trees close together; grass and rough herbage at foot, with large bramble patches nearby
(80) *Berwick Bassett 2*, 2F Rough herbage	Concreted dry dewpond, surrounded by large nettle patch; cultivation on one side, open downland on the other
(81) *Berwick Bassett 3*, 3F Rough herbage	Long grass and rough herbage with two sarsens at the foot of a wire fence separating two pastures
(82) *Shoulder of Mutton 1*, 3G Beech (dense)	Beechwood, with at the time of collection (1951) much leaf litter, and some nettles at and near the south end. Since then, cattle-trampled, and now far greener
(83) *Shoulder of Mutton 2*, 3G Nettles-in-grass	Small hollow with rough herbage, mainly nettles, surrounded by downland grass (rather short)
(84) *Shoulder of Mutton 3*, 3G Nettles-in-grass	Small scattered nettle patches on short downland turf on steep slope
(85) *Shoulder of Mutton 4*, 3G Nettles-in-grass	Open downland, with a few large clumps of nettles, and a few other broad-leaved herbs
(86) *Shoulder of Mutton 5*, 3G Nettles-in-grass	Open downland, with a few large clumps of nettle

(87) *Rockley Down 1*, 5F Beech (dense)	North end of beech wind-break. Fairly dense, with many low elders. Much beech litter on ground
(88) *Rockley Down 2*, 5F Beech (dense)	South end of beech wind-break. Fairly dense plantation of beeches. About one-third of the collecting area with many elders in a continuous stretch. Remainder with much short grass, almost continuous cover. Very little beech-litter
(89) *Rockley Down 3*, 4F Nettles-in-grass	Very steep downland slope. Regressing warren with a few large earths (? fox). Short grass with exposure of pale soil. Many nettle clumps and a few umbellifers
(90) *Dean Bottom 1*, 5F Long grass	Long downland grass on bank, very few herbs. Cultivation above bank, gallop below
(91) *Dean Bottom 2*, 5F Long grass	Long downland grass on bank, with strong mixture of coarse herbs (umbellifers, thistles, some nettles)
(92) *Dean Bottom 3*, 5F Long grass	Fairly steep open downland
(93) *Dean Bottom 4*, 5G Long grass	Long downland grass on bank, with strong mixture of thistles and other herbs
(94) *Dean Bottom 5*, 5G Nettles-in-grass	Small nettle patch (*ca.* 3×2 m) in long downland grass with few herbs
(95) *Dean Windbreak 1*, 4G Beech (open)	North end of a long windbreak; conifers and beeches mixed. Ground rather bare, mainly because of conifer litter. Some grass and a little scattered rough herbage. Cultivation all around
(96) *Dean Windbreak 2*, 4G Beech (open)	South end of long wind-break. Beeches, some conifers. At ground level almost entirely short grass and nettles. Some shading by scattered elders
(97) *Preshute Down*, 4H Nettles-in-grass	Regressing warren on very steep downland. Many nettles
(98) *Sharpridge 1*, 3H Nettles-in-grass	Alongside the Ridgeway. Small clumps of nettles and rough herbage in grass, shaded by edge of a beech clump in which no snails were found; cultivation on east side of Ridgeway, open downland (cattle-pasture) on the west
(99) *Sharpridge 2*, 3H Rough herbage	Alongside the Ridgeway. Small clumps of nettles and rough herbage in long grass. Cultivation on both sides of Ridgeway
(100) *Sharpridge 3*, 3H Rough herbage	As Sharpridge 1, but cultivation on north-west, open downland on north-east of Ridgeway
(101) *Sharpridge 4*, 2G Nettles-in-grass	Patch of rough herbage (nettles and thistles) surrounded by open downland

(102)	*Walker's Plantation*, 2H Mixed deciduous wood	Small mixed deciduous copse, merging into a conifer plantation; many elders with bare earth beneath. Open downland on one side, cultivation on the others
(103)	*Rockley North 1*, 6E Mixed deciduous wood	Elders by roadside, with very thick undergrowth of nettles. Beechwood until 1945, when cut down (*fide* P. M. Sheppard)
(104)	*Rockley North 2*, 6E Beech (dense)	Dense beechwood, with very little herb layer. Much beech litter (leaves and cupules)
(105)	*Rockley North 3*, 6E Beech (dense)	Fairly dense beechwood, with leaf litter and some grass and elders (greener than in Rockley North 2)
(106)	*Rockley North 4*, 5E Long grass	Steep-sided grassy bank alongside stony track by beechwood. Thrush-stones under isolated small thorn bushes
(107)	*Cemetery 1*, 7E Rough herbage	Nettles and rough herbage in long downland grass. Surrounded by gallops and open downland, except for cultivation on the south-east
(108)	*Cemetery 2*, 7E Rough herbage	As Cemetery 1, in a slight depression
(109)	*Middle Track 1*, 5G Rough herbage	Remains of burnt rick with some large stones overgrown with short grass and much nettle. Gallop on one side, cultivation on the other
(110)	*Middle Track 2*, 5G Nettles-in-grass	Small area of relict open downland beside gallop, and next to cultivation. Many nettle clumps near track
(111)	*Middle Track 3*, 5G Short turf	Gallop with cultivation all round and inside
(112)	*Barbury Castle 1*, 5I Gorses (grass)	Large patches of gorse, paths between the clumps heavily cattle-trampled. Surrounded by open downland
(113)	*Barbury Castle 2*, 5I Short turf	As Barbury Castle 3
(114)	*Barbury Castle, 3* 4I Short turf	Steep sides and bottom of large Iron Age earthwork; short turf, some exposures of soil in the steepest parts. Surrounded by downland
(115)	*Barbury Castle 4*, 4I Short turf	As Barbury Castle 3
(116)	*Barbury Castle 5*, 4I Rough herbage	Small area of rough herbage and grass (beginning of an old track) with open downland on one side, and sown pasture on the other
(117)	*Barbury Castle 6*, 4H Long grass	Old dewpond, still with water, at edge of cultivated field, with a little grass and rough herbage around it. Adjacent to track, beyond which is open downland

(118) *Barbury Road 2*, 4I Long grass	East side of metalled road. Mainly a grass bank with a hedge above and some rough herbage; beyond the hedge, open downland
(119) *Barbury Road 3*, 4I Long grass	East side of metalled road, contiguous with Barbury Road 2. Grassy bank, a few very scattered thorn bushes
(120) *Barbury Road 5*, 4I Rough herbage	West side of metalled road. Wide, flat, very grassy near road, then with much rough herbage extending up a steep bank. Cultivation beyond
(121) *Barbury Road 6*, 4I Rough herbage	West side of metalled road, separated by a small bare area from Barbury Road 5; much rough herbage, some grass near road. Cultivation beyond
(122) *Barbury Road 7*, 4I Long grass	Rough grass and one thorn bush, on broad track leading down from the Ridgeway. Cultivation on both sides
(123) *Barbury Road 8*, 4I Mixed deciduous wood	Small patch of old thorns in the middle of a cultivated field, about 40 m from the Ridgeway. Mainly grass, some nettle. Ploughed up since the collection, colony now extinct
(124) *Barbury Road 9*, 4I Long grass	Bare patch of chalk (remains of the excavation of a tumulus) surrounded by long downland grass, beside the Ridgeway. Sown pasture to the south, cultivation to the north, open downland to the east
(125) *Uffcott Down*, 3I Long grass	Track in cutting on downland scarp. Long grass, some rough herbage, a few small thorns
(126) *Maizey Down 1*, 6H Rough herbage	Old chalk pit. Mainly grass and rough herbage with a single elder and some brambles. Surrounded by open downland
(127) *Maizey Down 2*, 6G Nettles-in-grass	Regressing warren on rather steep downland. Downland grass with many scattered nettle clumps
(128) *Maizey Down 3*, 6G Nettles-in-grass	Regressing warren on open downland, with scattered nettle clumps
(129) *Maizey Down 4*, 6G Hedgerow	A broken line of old thorns (remains of a hedge) with grass, rough herbage and some brambles. On grass verge beside road, surrounded by downland, with open mixed deciduous clump nearby. Thrush stone sample
(130) *Maizey Down 5*, 6G Long grass	Open downland with very scattered gorse and elders. A little rough herbage
(131) *Smeathe's Ridge 1*, 5I Mixed deciduous wood (open)	Small open wood with conifers. Very grassy with many elders, hawthorns and brambles. Cultivation on east side, downland on the rest

(132)	*Smeathe's Ridge 2*, 5H Hedgerow	Patch of thick brambles (*ca.* 25 × 5 m), beside wide downland track, cultivation on three sides, downland on other side of track. Now ploughed up
(133)	*Smeathe's Ridge 3*, 6H Long grass	Scattered clumps of gorse with some brambles on open downland; grass between the clumps. Now ploughed up
(134)	*Smeathe's Ridge 4*, 6H Long grass	Edge of regressing warren on steep downland. Almost entirely tussocks of grass. Small patch of elders nearby. Very little rough herbage
(135)	*Burderop Down 1*, 6I Rough herbage	Very dense and extensive nettle patch in old chalkpit; open downland on three sides, cultivation on the north
(136)	*Burderop Down 2*, 6I Short turf	Side of down, open downland
(137)	*Burderop Down 3*, 7I Rough herbage	Triangular patch (*ca.* 20 × 10 m) with many thorns forming a hedge around it; some brambles, much rough herbage, mainly nettles
(138)	*Burderop Down 4*, 5I Hedgerow	Old hedge of elder trees, some thorns, and some brambles, on wide grass verge of Ridgeway. Cultivation on both sides
(139)	*Coombe Down 1*, 8G Mixed	Very small pit with thorns and brambles, a little gorse. Surrounded by open downland
(140)	*Coombe Down 2*, 7G Nettles-in-grass	Nettle patch surrounded by open downland, probably regressing warren
(141)	*Coombe Down 3*, 7G Mixed deciduous wood (open)	Mixed deciduous and coniferous plantation, very open; much rough herbage (nettles, etc.) and brambles, some grass. Surrounded by cultivation; surrounding field very recently ploughed up, probably open downland before
(142)	*Coombe Down 4*, 7H Rough herbage	Thrush stone in rough herbage and under elder, in overgrown pit of disused rifle range. Surrounded by downland
(143)	*Coombe Down 5*, 7H Long grass	Downland turf on sloping bank, former target area of rifle range
(144)	*Coombe Down 6*, 7H Long grass	As Coombe Down 5 and contiguous with it
(145)	*Hackpen Copse hedge*	Very sparse hedge of thorn bushes, with grass and bare earth beneath, alongside of Ridgeway. Cultivation on both sides

TABLE 1. COMPOSITION OF SAMPLES OF *CEPAEA NEMORALIS* FROM THE MARLBOROUGH DOWNS

			yellows					pinks					browns				
grid reference	locality	total	00000	00300	sp.-b.	5-banded	00345, etc.	00000	00300	sp.-b.	5-banded	00345, etc.	00000	00300	sp.-b.	5-banded	00345 etc.
123694	Crooked hedge	22	10	—	—	—	—	10	—	—	—	—	2	—	—	—	—
140692	Pickledean	39	—	—	9	—	—	5	3	19	—	—	—	2	1	—	—
131699	Parson's Penning 1	23	1	—	—	—	—	—	—	—	—	—	20	2	—	—	—
130699	2	24	1	—	—	—	—	—	—	—	—	—	18	5	—	—	—
128701	3	36	17	—	—	—	—	—	—	—	—	—	17	2	—	—	—
127706	4	24	2	—	—	—	—	6	—	—	—	—	14	2	—	—	—
126706	5	9	—	—	—	—	—	—	1	—	—	—	5	3	—	—	—
124703	6	51	11	7	—	—	—	6	6	1	—	—	17	3	—	—	—
130707	Overton Down 1	38	1	—	—	—	—	5	—	—	—	—	30	2	—	—	—
130710	2	50	—	1	—	—	—	—	—	—	—	—	45	3	1	—	—
136705	3	41	—	—	—	—	—	5	2	—	—	—	30	3	1	—	—
133706	4	31	—	—	—	—	—	6	2	—	—	—	21	2	—	—	—
134707	5	99	3	4	—	—	—	13	4	—	—	—	71	4	—	—	—
131710	6	46	1	—	—	—	—	4	1	—	—	—	39	1	—	—	—
134700	7	14	1	1	—	—	—	2	4	—	—	—	5	1	—	—	—
146700	Clatford Bottom 1	153	10	1	11	—	—	6	—	3	—	—	102	5	15	—	—
145704	2	81	12	—	13	—	—	8	—	—	—	—	36	5	7	—	—
142703	3	26	3	—	—	—	—	3	—	—	—	—	17	2	1	—	—
141705	4	79	14	—	—	—	—	14	1	—	—	—	48	2	—	—	—
140703	5	129	10	1	3	—	—	17	1	1	—	—	76	14	5	—	1
142702	6	4	1	—	—	—	—	—	—	—	—	—	3	—	—	—	—
151701	Devil's Den	58	11	2	1	—	—	11	1	1	—	—	26	2	3	—	—
134710	Delling 1	72	33	—	—	—	—	19	2	—	—	—	18	—	—	—	—
135707	2	75	19	3	—	—	—	4	7	—	—	—	38	3	1	—	—
136711	3	29	9	1	—	—	—	2	5	—	—	—	12	—	—	—	—
136708	4	41	6	2	—	—	—	4	5	—	—	—	22	2	—	—	—
137706	5	48	2	—	—	—	—	6	2	—	—	—	38	—	—	—	—
138710	Wroughton Copse	109	11	—	—	—	—	16	1	—	—	—	74	7	—	—	—
140713	Fyfield Down 1	29	3	1	—	—	—	1	1	—	—	—	21	2	—	—	—
140711	2	240	5	—	—	—	—	6	5	—	—	—	220	2	1	1	—
138712	3	53	4	3	—	—	—	2	4	—	—	—	35	5	—	—	—
136716	North Delling 1	14	1	4	—	—	—	2	—	—	—	—	5	2	—	—	—
137715	2	81	8	4	—	—	—	14	2	—	—	—	46	7	—	—	—
136713	3	79	14	—	—	—	—	28	6	—	—	—	24	7	—	—	—
132715	4	40	11	6	—	—	—	—	1	—	—	—	19	3	—	—	—
131713	5	35	13	1	—	—	—	3	2	—	—	—	14	2	—	—	—
127715	6	47	11	1	—	—	—	19	3	—	—	—	13	—	—	—	—
141718	Clatford Down 1	40	7	23	2	—	—	—	2	1	—	—	4	1	—	—	—
142716	2	52	4	3	—	—	—	5	2	—	—	—	30	8	—	—	—
139717	3	43	—	—	—	—	—	2	1	—	—	—	37	3	—	—	—
138717	4	19	2	6	—	—	—	—	—	—	—	—	11	—	—	—	—
145715	5	105	9	6	—	—	—	7	6	—	—	—	41	36	—	—	—
148713	6	125	12	4	2	—	—	22	34	4	—	—	44	2	1	—	—
146719	7	23	4	4	—	—	—	2	3	—	—	—	9	1	—	—	—
145719	8	11	3	5	—	—	—	—	—	—	—	—	3	—	—	—	—
144718	9	160	26	42	—	—	—	6	18	—	—	—	60	8	—	—	—
140722	Totterdown 1	35	14	8	—	—	—	3	4	—	—	—	6	—	—	—	—
139721	2	36	12	13	—	—	—	3	—	—	—	—	6	2	—	—	—
139719	3	23	3	10	—	—	—	—	3	—	—	—	6	1	—	—	—
135719	4	54	25	11	—	—	—	3	4	—	—	—	8	3	—	—	—
158718	Rockley 1	21	1	5	—	—	—	4	1	—	—	—	8	—	2	—	—
158717	2	140	18	15	1	—	—	52	7	—	—	—	45	2	—	—	—
156716	3	77	18	12	—	—	—	22	3	1	—	—	21	—	—	—	—
158716	4	110	22	16	1	—	—	19	10	—	—	—	42	—	—	—	—
159716	5	218	58	52	4	—	—	27	10	1	—	—	64	2	—	—	—
153716	6	91	9	6	—	—	—	12	19	—	—	—	45	—	—	—	—
152716	7	35	7	8	1	—	—	4	3	—	—	—	11	1	—	—	—
150716	8	40	3	4	1	—	—	8	6	1	—	—	15	1	1	—	—
148717	9	34	1	4	—	—	—	4	8	1	—	—	12	4	—	—	—
173706	Barton 1	59	8	30	5	—	—	—	2	14	—	—	—	—	—	—	—
168709	2	103	15	41	—	—	—	8	7	—	—	—	30	2	—	—	—
164710	3	97	19	21	4	—	—	8	15	3	—	—	25	2	—	—	—
164713	4	23	5	1	1	—	—	9	1	—	—	—	5	1	—	—	—
163712	5	26	9	2	—	—	—	5	6	—	—	—	3	1	—	—	—
162712	6	18	4	4	—	—	—	7	3	—	—	—	—	—	—	—	—
160712	7	6	1	1	—	—	—	4	—	—	—	—	—	—	—	—	—
160713	8	5	—	—	—	—	—	4	—	—	—	—	1	—	—	—	—
160715	9	35	7	8	—	—	—	7	2	—	—	—	9	2	—	—	—
181704	Rough Down	198	67	9	12	—	—	5	8	12	—	—	70	10	5	—	—
137728	Temple 1	6	1	3	—	—	—	2	—	—	—	—	—	—	—	—	—
137725	2	12	4	7	—	—	—	—	—	—	—	—	1	—	—	—	—
138724	3	6	4	—	—	—	—	—	2	—	—	—	—	—	—	—	—
140727	4	4	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—
142725	5	46	10	11	1	—	—	8	4	—	—	—	11	1	—	—	—
150724	6	8	—	7	—	—	—	—	—	—	—	—	1	—	—	—	—

Table 1 (*cont.*)

grid reference	locality	total	yellows					pinks					browns				
			00000	00300	sp.-b.	5-banded	00345, etc.	00000	00300	sp.-b.	5-banded	00345, etc.	00000	00300	sp.-b.	5-banded	00345, etc.
125728	Monkton Down 1	34	9	13	1	—	—	—	—	—	—	—	7	4	—	—	—
118725	3	23	10	3	8	—	—	—	—	—	—	—	2	—	—	—	—
116726	5	38	12	18	4	—	—	1	—	—	—	—	2	1	—	—	—
125730	6	5	1	—	—	—	—	4	—	—	—	—	—	—	—	—	—
124737	Berwick Bassett 1	94	20	64	—	—	—	8	2	—	—	—	—	—	—	—	—
126738	2	21	—	16	—	—	—	—	5	—	—	—	—	—	—	—	—
131737	3	21	11	4	—	—	—	6	—	—	—	—	—	—	—	—	—
132743	Shoulder of Mutton 1	158	15	23	1	—	—	78	39	—	—	—	1	1	—	—	—
133744	2	28	—	18	—	—	—	1	9	—	—	—	—	—	—	—	—
134743	3	5	—	5	—	—	—	—	—	—	—	—	—	—	—	—	—
131741	4	94	9	38	—	1	—	29	12	—	1	—	4	—	—	—	—
130741	5	7	—	1	—	—	—	5	1	—	—	—	—	—	—	—	—
155734	Rockley Down 1	27	3	2	1	1	—	1	—	—	—	—	18	1	—	—	—
153730	2	80	6	5	—	—	—	5	3	—	—	—	55	6	—	—	—
145736	3	292	14	270	—	—	—	—	—	—	—	—	7	1	—	—	—
156735	Dean Bottom 1	41	7	4	—	—	—	2	—	—	—	—	21	7	—	—	—
156736	2	49	7	18	1	—	—	1	—	—	—	—	21	1	—	—	—
156737	3	39	15	14	—	—	—	1	—	—	—	—	9	—	—	—	—
154740	4	53	17	23	—	—	—	—	—	—	—	—	12	1	—	—	—
152742	5	51	6	40	—	—	—	—	—	—	—	—	5	—	—	—	—
148747	Dean Windbreak 1	25	1	20	—	—	—	1	3	—	—	—	—	—	—	—	—
144741	2	173	5	168	—	—	—	—	—	—	—	—	—	—	—	—	—
144750	Preshute Down	25	2	20	—	—	—	3	—	—	—	—	—	—	—	—	—
131751	Sharpridge 1	16	8	7	—	—	—	—	1	—	—	—	—	—	—	—	—
134755	2	96	—	26	—	—	—	70	—	—	—	—	—	—	—	—	—
136758	3	46	4	32	—	—	—	10	—	—	—	—	—	—	—	—	—
128748	4	8	4	4	—	—	—	—	—	—	—	—	—	—	—	—	—
129757	Walker's Plantation	4	—	3	—	—	—	1	—	—	—	—	—	—	—	—	—
166726	Rockley North 1	88	11	15	—	3	1	16	16	1	5	1	18	1	—	—	—
161727	2	107	9	3	—	3	—	15	17	2	6	—	52	—	—	—	—
161725	3	59	7	5	1	3	—	5	21	—	2	—	14	1	—	—	—
158724	4	50	7	11	—	1	1	2	12	—	3	—	13	—	—	—	—
172726	Cemetery 1	6	4	—	—	1	—	1	—	—	—	—	—	—	—	—	—
171727	2	34	9	5	—	6	4	1	2	—	5	2	—	—	—	—	—
152747	Middle Track 1	17	—	10	—	4	—	—	3	—	—	—	—	—	—	—	—
151748	2	12	1	11	—	—	—	—	—	—	—	—	—	—	—	—	—
154745	3	5	—	2	—	3	—	—	—	—	—	—	—	—	—	—	—
151763	Barbury Castle 1	26	4	—	—	14	—	2	—	—	6	—	—	—	—	—	—
150764	2	6	—	—	—	4	—	—	—	—	2	—	—	—	—	—	—
148764	3	75	13	1	—	25	3	6	—	—	6	—	3	—	—	18	—
149762	4	40	3	8	—	11	—	6	2	—	6	1	2	1	—	—	—
147760	5	59	16	21	—	4	—	4	9	—	—	—	1	4	—	—	—
147758	6	23	5	11	—	—	—	3	3	—	—	—	—	—	—	1	—
146767	Barbury Road 2	18	1	—	—	2	—	4	3	—	7	—	1	—	—	—	—
146766	3	74	1	5	—	10	—	15	10	1	30	1	—	1	—	—	—
146767	5	10	2	1	—	1	—	2	—	—	3	—	—	1	—	—	—
146766	6	37	2	2	—	3	—	9	3	—	18	—	—	—	—	—	—
143765	7	24	4	6	3	—	—	8	1	—	—	—	—	1	—	1	—
143764	8	46	13	15	—	1	—	8	7	1	—	—	—	1	—	—	—
145763	9	21	1	5	—	2	—	4	3	—	3	—	—	3	—	—	—
139768	Uffcott Down	39	1	5	1	20	—	3	2	—	7	—	—	—	—	—	—
164751	Maizey Down 1	48	2	19	—	8	—	—	13	—	6	—	—	—	—	—	—
163749	2	53	8	16	—	22	2	1	3	—	1	—	—	—	—	—	—
162749	3	16	2	8	—	1	1	2	1	—	—	1	—	—	—	—	—
165746	4	42	2	9	—	9	2	13	6	—	1	—	—	—	—	—	—
164742	5	114	—	22	—	34	—	42	6	—	10	—	—	—	—	—	—
158761	Smeathe's Ridge 1	22	—	3	—	14	—	1	—	—	3	—	1	—	—	—	—
160758	2	9	3	—	—	2	—	—	1	—	3	—	—	—	—	—	—
161756	3	68	20	21	—	6	—	9	12	—	—	—	—	—	—	—	—
167756	4	54	—	—	—	15	—	7	—	—	31	—	—	—	—	1	—
164767	Burderop Down 1	63	—	—	—	47	3	—	—	—	13	—	—	—	—	—	—
165765	2	10	—	—	—	6	1	1	—	—	2	—	—	—	—	—	—
171764	3	38	3	—	—	24	2	2	—	—	7	—	—	—	—	—	—
157769	4	68	5	2	—	46	—	2	3	—	10	—	—	—	—	—	—
181746	Coombe Down 1	11	—	—	—	11	—	—	—	—	—	—	—	—	—	—	—
179745	2	33	—	—	—	26	1	—	—	—	5	1	—	—	—	—	—
176747	3	7	—	—	—	4	—	—	—	—	3	—	—	—	—	—	—
179750	4	88	—	—	—	63	13	—	—	—	12	—	—	—	—	—	—
179750	5	66	—	1	—	53	10	—	—	—	2	—	—	—	—	—	—
179750	6	72	—	1	—	56	13	—	—	—	1	1	—	—	—	—	—
168774	Hackpen Copse hedge	18	—	2	—	5	—	—	4	—	7	—	—	—	—	—	—

sp.-b. = spread-banded.

TABLE 2. STABILITY OF PHENOTYPE COMPOSITION IN POPULATIONS OF *CEPAEA*

(i) *CEPAEA NEMORALIS*

			yellows					pinks					browns				
locality	date	total	00000	00300	sp.-b.	5-banded	00345 etc.	00000	00300	sp.b.	5-banded	00345 etc.	00000	00300	sp.-b.	5-banded	0034 etc.
Rough Down	1949	164	47	27		—	—	5	20		—	—	49	16		—	—
	1950	67	29	6		—	—	1	3		—	—	18	—		—	—
	1951	70	31	7		—	—	1	10		—	—	24	6		—	—
	1960	198	67	21		—	—	5	20		—	—	70	15		—	—
Rockley 2	1951	140	18	15	1	—	—	52	7	—	—	—	45	2	—	—	—
	1961	111	7	4	—	—	—	39	10	—	—	—	51	—	—	—	—
Rockley 3	1951	77	18	12	—	—	—	22	3	1	—	—	21	—	—	—	—
	1961	105	24	24	—	—	—	30	6	—	—	—	21	—	—	—	—
Rockley 5	1951	218	58	52	4	—	—	27	10	1	—	—	64	2	—	—	—
	1956	80	26	19	2	—	—	12	2	1	—	—	17	—	1	—	—
Shoulder of Mutton Plantation	1949	158	15	23	1	—	—	78	39	—	—	—	1	1	—	—	—
	1954	36	4	5	—	—	—	20	5	—	—	—	1	1	—	—	—
	1960	12	1	—	—	—	—	7	3	—	—	—	1	—	—	—	—
Sharpridge 2	1958	19	—	7	—	—	—	12	—	—	—	—	—	—	—	—	—
	1959	96	—	26	—	—	—	70	—	—	—	—	—	—	—	—	—
	1960	33	—	10	—	—	—	23	—	—	—	—	—	—	—	—	—
	1961	34	—	8	—	—	—	26	—	—	—	—	—	—	—	—	—
Dewdrop Covert 2, Lambourn	1954	44	2	1	2		—	8	26	5		—	—	—	—	—	—
	1960	206	10	26	3	2	—	18	120	1	25	—	1	—	—	—	—
Canal Bank, Oxford	1949	104	8	16	—	28	6	—	8	—	36	1	1	—	—	—	—
	1958	33	6	1	—	11	—	2	1	—	12	—	—	—	—	—	—

(ii) *CEPAEA HORTENSIS*

locality	date	total	12345	5-banded with fusion	00000	02345	10345	10305	10045	10005	00345	00340	00045	00005
Oare Hill (all yellows)	1950	217	105	27	17	1	18	2	6	17	3	1	3	17
	1957	48	25	6	2	—	—	—	5	6	—	—	—	4
	1961	64	36	3	7	—	4	—	1	8	—	—	—	5

sp.-b. = spread-banded.

TABLE 3. COMPOSITION OF SAMPLES OF *CEPAEA NEMORALIS* FROM THE LAMBOURN DOWNS

			yellows					pinks					browns				
grid reference	locality	total	00000	00300	sp.-b.	5-banded	00345, etc.	00000	00300	sp.-b.	5-banded	00345, etc.	00000	00300	sp.-b.	5-banded	00345, etc.
Beechwoods																	
SU 331821	Dewdrop Covert 2	206	10	26	3	2	—	18	120	1	25	—	1	—	—	—	—
332822	Dewdrop Covert 1	12	1	3	—	1	—	1	6	—	—	—	—	—	—	—	—
332826	Long Covert 3	30	1	8	—	1	—	1	7	—	2	—	9	1	—	—	—
332827	Long Covert 2	304	9	36	7	16	—	41	85	4	29	1	73	—	3	—	—
333828	Long Covert 1	78	2	20	4	6	1	21	8	1	1	—	12	—	2	—	—
331830	Old Warren 1	114	8	25	9	1	—	15	43	6	7	—	—	—	—	—	—
332831	Old Warren 2	162	24	67	14	1	—	12	40	1	2	—	—	—	1	—	—
333832	Old Warren 3	68	12	34	2	—	—	6	13	1	—	—	—	—	—	—	—
336833	Triangle Clump 1	211	59	132	6	13	—	—	—	—	1	—	—	—	—	—	—
336834	Triangle Clump 2	135	35	86	2	8	—	2	2	—	—	—	—	—	—	—	—
337834	Boundary Covert 1	120	2	46	5	31	—	—	19	—	17	—	—	—	—	—	—
338836	Boundary Covert 2	135	6	50	11	31	1	1	23	1	11	—	—	—	—	—	—
338837	Boundary Covert 3	239	47	104	14	39	1	1	22	1	10	—	—	—	—	—	—
339840	Clump 3 West side of road	52	4	36	1	6	—	—	5	—	—	—	—	—	—	—	—
340844	Sparsholt Firs 3	41	2	16	2	1	—	—	18	—	—	—	2	—	—	—	—
341846	Sparsholt Firs 2	59	2	22	—	—	—	1	26	1	2	—	5	—	—	—	—
343851	Sparsholt Firs 1	77	2	4	9	5	—	12	30	10	5	—	—	—	—	—	—
311864	Rams Hill Plantation 1	34	1	14	8	9	—	—	1	1	—	—	—	—	—	—	—
308858	Rams Hill Plantation 2	37	—	8	2	1	—	18	3	4	—	1	—	—	—	—	—
334856	Rubblepit Plantation	30	—	14	4	11	1	—	—	—	—	—	—	—	—	—	—
Grassland and rough herbage																	
333818	Lambourn Roadside	33	7	12	13	1	—	—	—	—	—	—	—	—	—	—	—
329827	Seven Barrows 1	108	25	25	5	13	—	30	6	3	—	—	1	—	—	—	—
329828	Seven Barrows 2	74	13	23	3	4	—	19	9	1	2	—	—	—	—	—	—
330829	Seven Barrows 3	63	12	19	12	5	1	5	2	1	3	—	3	—	—	—	—
346852	Pigtrough Roadside 1	143	44	53	16	3	—	5	14	4	4	—	—	—	—	—	—
347853	Pigtrough Roadside 2	25	6	6	3	7	—	1	1	—	1	—	—	—	—	—	—
352855	Sincombe Farm 2	101	1	73	13	4	—	10	—	—	—	—	—	—	—	—	—
354857	Sincombe Farm 1	26	—	20	5	1	—	—	—	—	—	—	—	—	—	—	—
305857	Uffington Down	49	—	14	19	6	—	—	3	3	4	—	—	—	—	—	—
300863	Uffington Castle	29	—	12	6	3	1	—	4	1	1	—	—	—	1	—	—

sp.-b. = spread-banded.

Table 4. Composition of samples of *Cepaea nemoralis* from various localities

grid reference	locality	total	yellows					pinks					browns				
			00000	00300	sp.-b.	5-banded	00345 etc.	00000	00300	sp.-b.	5-banded	00345 etc.	00000	00300	sp.-b.	5-banded	00345 etc.
							higher chalk downs and grassland										
ST 887509	Beggar's Knoll	122	24	8	—	36	3	10	6	—	34	1	—	—	—	—	—
SU 044557	Dogtail Down	44	—	11	—	—	—	19	14	—	—	—	—	—	—	—	—
SU 006656	King's Play Hill 1	74	—	—	—	4	—	2	3	—	32	—	12	—	1	19	1
SU 004657	King's Play Hill 2	17	—	1	—	5	—	2	2	1	4	—	1	—	—	1	—
ST 995657	Heddington Beacon 2	66	—	8	—	5	—	8	12	—	30	—	—	1	—	2	—
SU 385845	Segsbury Camp	64	1	7	1	44	2	—	2	—	6	—	1	—	—	—	—
SU 065542	Chirton Down 1	48	1	23	2	9	—	1	12	—	—	—	—	—	—	—	—
SU 063537	Chirton Down 2	80	1	35	5	6	—	1	24	3	5	—	—	—	—	—	—
SU 462575	Beacon Hill Fort	33	—	—	—	3	—	2	—	—	27	1	—	—	—	—	—
TQ514645	The Roundel Lullingstone	261	—	8	—	55	6	10	14	—	158	10	—	—	—	—	—
SU 225824	Callas Hill	21	—	1	—	10	—	3	1	—	6	—	—	—	—	—	—
SU 102525	Water Dean Bottom 2	30	—	8	3	5	—	—	8	2	4	—	—	—	—	—	—
SU 208797	Liddington Castle	23	1	11	—	9	1	—	—	—	1	—	—	—	—	—	—
							other habitats from higher chalk										
TQ520638	Beechen Wood (beech)	23	—	1	—	4	—	2	4	—	12	—	—	—	—	—	—
SU 073693	Knoll Down (open wood)	33	—	—	4	—	—	—	4	2	—	—	17	—	6	—	—
SU 075693	Knoll Down roadside (open wood)	82	—	—	3	—	—	2	6	8	—	—	45	1	17	—	—
SU 045558	Dogtail Plantation (mixed deciduous wood)	87	2	16	—	6	—	19	30	—	14	—	—	—	—	—	—
ST 969530	Erlestoke (mixed deciduous wood)	64	—	2	—	7	—	35	3	4	9	—	4	—	—	—	—
SU 110629	Walker's Hill (rough herbage)	7	5	—	—	—	—	1	—	—	—	—	1	—	—	—	—
SU 064539	Chirton Down Wood (mixed deciduous wood)	94	—	36	2	10	—	3	30	—	13	—	—	—	—	—	—
							lower chalk and adjacent formations										
SU 052750	Clevancy Wood (beech)	21	—	—	—	—	—	1	—	—	8	—	11	1	—	—	—
SU 147797	Wroughton South (mixed)	11	—	—	—	5	1	—	—	—	5	—	—	—	—	—	—
SU 376874	Windmill Hill (hedgerow)	72	7	1	—	33	—	2	—	—	4	—	24	—	—	—	1
SU 483823	Hodcott Down 1 (grass)	27	—	2	—	6	3	—	3	—	7	6	—	—	—	—	—
SU 483824	Hodcott Down 2 (grass)	20	—	3	—	4	2	—	4	—	7	—	—	—	—	—	—
SU 182784	Chisledon Camp corner (hedgerow)	29	5	3	—	15	—	—	—	—	6	—	—	—	—	—	—
SU 222808	Shepherds Rest (hedgerow)	69	—	9	—	35	7	—	—	—	17	1	—	—	—	—	—
SU 244798	Wanborough Plain (hedgerow)	30	—	—	—	2	—	1	—	—	27	—	—	—	—	—	—
ST 976537	nr. Erlestoke (hedgerow)	4	—	—	—	—	—	1	1	—	1	—	—	—	—	1	—
							limestones										
SP 106296	Trafalgar Wood (edge of beechwood)	27	—	1	1	3	1	3	3	4	3	8	—	—	—	—	—
SP 104315	Ling Ground Quarry (grass)	35	1	2	—	16	9	—	—	—	4	3	—	—	—	—	—
SP 209105	Leyes Farm Wood (mixed deciduous wood)	81	—	26	—	43	—	—	2	—	10	—	—	—	—	—	—
ST 843753	Ford 1 (beechwood)	51	—	2	—	—	—	12	5	1	3	—	26	1	—	1	—
ST 842755	Ford 2 (mixed deciduous wood)	17	—	—	—	—	—	—	5	—	7	—	4	—	—	1	—
ST 843755	Ford 3 (mixed)	6	—	—	—	—	—	1	4	—	1	—	—	—	—	—	—
ST 556738	Leigh Wood, wood (mixed deciduous wood)	78	1	1	2	4	—	6	21	7	20	3	10	—	1	2	—
ST 553737	Leigh Wood, path (mixed deciduous wood)	51	—	1	1	3	—	3	21	1	11	7	3	—	—	—	—
ST 474546	Cheddar Gorge (mixed)	53	—	3	—	19	—	—	1	—	29	1	—	—	—	—	—
SO 977396	Bredon Hill Wood (beech)	49	—	—	—	20	6	2	—	—	9	5	4	—	—	1	2
SO 978395	Bredon Hill grass	63	—	2	—	46	4	—	1	—	10	—	—	—	—	—	—
SO 977397	Bredon Hill thorns (mixed)	54	—	2	—	26	10	—	—	—	14	2	—	—	—	—	—

TABLE 4 (*cont.*)

			yellows					pinks					browns				
grid reference	locality	total	00000	00300	sp.-b.	5-banded	00345 etc.	00000	00300	sp.-b.	5-banded	00345 etc.	00000	00300	sp.-b.	5-banded	00345 etc.
							other formations										
SU 226668	Eight Walks, Savernake (mixed deciduous wood)	31	—	—	—	1	—	4	8	13	5	—	—	—	—	—	—
SP 504058	Osney Cemetery (rough herbage)	174	—	5	—	127	5	—	1	—	35	1	—	—	—	—	—
SW 871331	Roseland Peninsula (rough herbage)	85	30	—	—	25	8	6	—	—	6	9	1	—	—	—	—
SX 017449	Mevagissey (rough herbage)	170	8	105	—	52	1	—	1	—	3	—	—	—	—	—	—
SP 493255	Heyford Canal (rough herbage)	132	23	13	—	31	—	7	6	—	24	1	27	—	—	—	—
SP 568162	Charlton on Otmoor (hedgerow)	92	1	9	—	35	4	—	3	—	40	—	—	—	—	—	—
SP 283007	Friar's Court (hedgerow)	48	1	12	—	15	—	2	3	—	2	—	12	—	—	1	—
SP 557862	Boston Farm, Lutterworth (hedgerow)	106	—	19	—	19	—	1	26	—	39	—	1	1	—	—	—
SP 675106	Hornage Farm (rough herbage)	19	—	5	—	3	—	5	3	—	3	—	—	—	—	—	—
SP 571128	Otmoor-Beckley (rough herbage)	37	9	1	—	6	1	4	2	—	14	—	—	—	—	—	—
SP 665052	Rycote (rough herbage)	361	50	—	—	68	1	144	1	—	95	—	2	—	—	—	—

sp.-b = spread-banded.

TABLE 5. FREQUENCIES OF A RECESSIVE ALLELOMORPH IN HETEROTIC EQUILIBRIUM FOR DIFFERENT INTENSITIES OF PHYSIOLOGICAL AND VISUAL SELECTION

C = visual selection on recessive	0·90	0·95	0·99	1·00	1·01	1·05	1·10
	−10 %	−5 %	−1 %	0	+1 %	+5 %	+10 %
$a = c = 0{\cdot}999$, physiological selection on homozygotes −0·1 %	0·0098	0·0192	0·0834	0·500	1·0	1·0	1·0
$a = c = 0{\cdot}990$, −1 %	0·084	0·144	0·334	0·500	0·990	1·0	1·0
$a = c = 0{\cdot}950$, −5 %	0·256	0·339	0·457	0·500	0·552	0·952	1·0
$a = c = 0{\cdot}900$, −10 %	0·345	0·417	0·478	0·500	0·524	0·645	0·909

TABLE 6. COMPOSITION OF SAMPLES OF *CEPAEA HORTENSIS*

locality	total	yellow 00000	% yellow 00000	yellow '12345'	'fusions'	% 'fusions'/ '12345'	pinks and browns (*p*), (*b*)
	(i) Samples of *Cepaea hortensis* from the Marlborough Downs						
Crooked Hedge	32	12	37·5	19	1	5·0	—
Clatford Bottom 1	143	28	19·6	101	14	12·2	—
Walker's Plantation	24	3	12·5	14	7	33·3	—
Temple 4	8	2	25·0	4	2	33·3	—
Cemetery 1	9	3	33·3	5	0	0·0	1*p* 00000
Burderop Down 4	27	0	0·0	8	19	70·4	—
Nut Plantation Hedge 2	43	13	30·2	22	8	26·7	—
Smeathe's Ridge 1	22	14	63·6	7	1	12·5	—
Temple 1	30	3	10·0	20	7	25·9	—
Monkton Down 1	6	5	83·3	1	0	0·0	—
Monkton Down 5	121	28	23·1	65	27	30·1	1*p* 12345
Nr Monkton Down 5	79	19	24·1	44	15	25·4	1*p* 00000
Monkton Down 6	22	10	45·5	11	1	8·3	—
Fiddler's Hill	34	7	20·6	18	6	29·6	1*p* 12345 + 2*p* 'fusions'

Table 6 (*cont.*)

locality	total	yellow 00000	% yellow 00000	yellow '12345'	'fusions'	% 'fusions'/ '12345'	pinks and browns (*p*), (*b*)
Barbury Road 1	34	11	32·4	18	5	21·7	—
Barbury Road 4	19	5	26·3	12	2	14·3	—
Barbury Road 5	10	1	10·0	8	1	11·1	—
Cemetery 2	9	0	0·0	9	0	0·0	—
Wedgwood Field	13	3	23·1	9	1	10·0	—
Barton Copse Hedgerow	6	1	16·7	4	1	20·0	—
Uffcott Down	25	13	52·0	11	1	8·3	—
Overton Down 7	9	3	33·3	2	3	66·7	1*b* 'fusion'
Clatford Down 6	79	0	0·0	60	19	24·1	—
Totterdown 3	21	5	23·8	13	3	18·8	—
Down Barn 2	44	22	50·0	17	5	22·7	—
Pickledean Bottom 1	29	2	6·9	23	4	14·8	—
Temple 6	105	84	80·0	11	10	47·6	—
Wroughton Copse	232	119	51·3	104	8	7·1	1*b* 00000
Clatford Bottom 4	28	1	3·6	26	1	3·7	—
Rockley North 4	53	14	26·4	5	34	89·7	—
Og Valley 1	27	8	29·6	8	9	52·6	1*p* 12345; 1*p* 'fusion'
Ogbourn Camp Hedge	25	0	0·0	14	10	44·0	1*p* 'fusion'

Grid references of all localities not shared with *C. nemoralis*: Fiddler's Hill, SU 124751; Wedgwood Field, SU 183698; Barton Copse Hedgerow, SU 171697; Down Barn 2, SU 133699; Pickledean Bottom 1, SU 133694; Barbury Road 1, SU 145766; Near Monkton Down 5, SU 115726.

(ii) Samples from elsewhere

locality	total	yellow 00000	% yellow 00000	yellow '12345'	'fusions'	% 'fusions'/ '12345'	pinks and browns (*p*), (*b*)
Walker's Hill	90	11	12·2	23	18	61·6	6*p* 00000, 5*p* 12345 27*p* 'fusions'
North of Barbury Castle	20	8	40·0	12	0	0·0	—
Erlestoke	22	7	31·8	7	7	50·0	1*p* 00000
Og Valley 2	21	17	81·0	3	0	25·0	—
Burderop Hackpen	46	25	54·3	11	10	47·6	—
Wroughton South	18	1	5·6	7	10	58·8	—
Hedge nr. Erlestoke	10	1	10·0	2	5	71·4	1*p* 00000, 1*b* 00000
Sincombe Farm 1	83	6	7·2	77	15	19·5	55 are hyalozonate
Knoll Down	9	2	22·2	2	5	71·4	—
Hodcott Down 1	30	0	0·0	26	4	13·3	—
Hodcott Down 3	34	0	0·0	30	4	11·8	—
Gibbet Knoll	40	28	70·0	7	4	36·4	1*p* 00000
King's Play Hill Hedge	5	2	40·0	1	2	66·7	—
Dewdrop Covert 1	156	1	0·6	116	39	25·2	13 are hyalozonate
Bratton White Horse	36	22	61·1	9	5	35·7	—
Heddington Beacon 1	25	9	36·0	12	4	25·0	—
Heddington Beacon 2	61	12	19·7	10	39	79·6	—

Grid references: North of Barbury Castle, SU 145775; Erlestoke, ST 977536; Og Valley 2, SU 196725; Burderop Hackpen, SU 174779; Wroughton South, SU 147797; Hedge nr. Erlestoke, ST 996537; Sincombe Farm 1, SU 354857; Knoll Down, SU 073693; Hodcott Down 1, SU 483823; Hodcott Down 3, SU 483822; Gibbet Knoll, SU 028534; King's Play Hill Hedge, SU 005657; Dewdrop Covert 1, SU 332822; Bratton White Horse, ST 897518; Heddington Beacon 1, ST 991659; Heddington Beacon 2, ST 995657.

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